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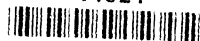
February, 1947

# THE JOURNAL OF ECOLOGY

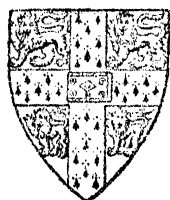
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BY  
W. H. PEARSALL

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# THE JOURNAL OF ECOLOGY

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## A VEGETATION MAP OF WESTERN PALESTINE

BY M. ZOHARY, *Department of Botany, Hebrew University, Jerusalem**(With one Map and one Figure in the Text)*

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## I. INTRODUCTION

In the following pages we give a condensed review of Palestine's plant communities. No details can be given here either on the ecological constitution of the habitat or on the floristical composition of the plant community.

A fair amount of information on Palestine's vegetation has been recently accumulated through the investigations of Eig (1927, 1931, 1933, 1938, 1939), Feinbrun & Zohary (1942), Zohary (1935, 1940*b*, 1941, 1944*a, b, c*), Zohary & Feinbrun (1942), and Zohary & Orshansky (1942*a, b*). Due to the war conditions only part of the results of this work has been published.

The plant communities recorded in this paper are only partly based upon analytical data; most of them were ascertained through field research and floristic records alone. It is therefore possible that nomenclature and hierarchical level of some minor phytosociological units mentioned below are subject to change in future more detailed studies. In delimitation of Palestine plant communities the vegetation units of the countries adjacent to the mapped area were also considered. Recent investigations in Transjordan, Sinai and Egypt, the results of which are still unpublished, have aided greatly to the understanding of the phytosociological relations of the area under review.

The phytosociological units and methods of research of the Zurich-Montpellier school have been followed; in presentation of the units an independent mode has

been adopted, which perhaps calls for elucidation. In the Mediterranean territory of Palestine, vegetation is affected by man to such an extent that the climax vegetation is strongly intermixed with vegetation of lower successional stages. Sometimes these stages prevail in considerable areas, arboreal climax vegetation being represented by scattered, meagre remnants solely. For that reason each vegetational area of the map has been based not only on its climax vegetation but also on one or more of the most permanent seral plant communities, leading to or derived from (through destruction) the climax association. In addition to the primary vegetation (permanent and climax plant communities) segetal vegetation has also been considered for each area. This type covers extensive stretches within the Mediterranean territory at present, and no true conception may be obtained of vegetation of the country if segetal plant communities are neglected. Moreover, in certain districts now wholly occupied by segetal plant communities, the climax vegetation is absolutely untraceable. The segetal vegetation, constituting a series of floristically and ecologically fairly well-defined plant communities, may add important features to the character of the vegetation areas considered.

This threefold method of presenting vegetation may, apart from its practical advantages, permit a deeper insight into the syngenetical relations of vegetation.

## II. TOPOGRAPHY

Palestine may be roughly divided into four longitudinal belts: the Coastal Plain, the Mountain Region, the Jordan Valley, and the Transjordan Plateau. Each of these has its particular climatical, edaphical and biogeographical characteristics.

The Coastal Plain comprises the light soil belt of Mediterranean Palestine. It does not exceed 200 m. in altitude. It is fringed on the west by a strip of sand dunes and traversed by a series of latitudinal water courses draining into the Mediterranean Sea.

The Mountain Region is made up mainly of Upper Cretaceous and Eocene limestone and chalk. Its highest peak reaches 1200 m. (Upper Galilee). It is intersected by a few latitudinal valleys, the most important of which are the Esdraelon Plain and the Valley of Beersheba. The western escarpments of the mountain ranges are Mediterranean in climate and vegetation, whereas the eastern slopes are steppes and deserts.

The Jordan Valley is the most significant orographical feature of the country. In altitude it ranges from 396 m. below sea-level (Dead Sea district) to 200 m. above sea-level (Dan Valley). It varies markedly in climate and vegetation according to altitude and geographical latitude. Swamps, salt marshes, and oases of tropical vegetation are most characteristic of this valley.

The Transjordan Plateau is cut in its western part by several latitudinal rivers and wadis emptying into the Jordan Valley and Dead Sea. While its western escarpments are very steep it gradually merges in the east into the Syrian Desert Plateau. In its northern half it is made up of calcareous rocks, while Nubian Sandstone and igneous rocks prevail in the south. The highest point is reached in Edom (1650 m. above sea-level).

## III. CLIMATE

Palestine is included within the subtropical climate zone designated by a rainy and mild winter and hot dry summer. This type of climate manifests in Palestine three well-marked variants: eu-Mediterranean, steppe and desert climate. The main ecological factor

designating these variants is the annual amount of rainfall, ranging in the Mediterranean between 300 and 1000 mm., in the steppe between 200 and 300 mm. and in the desert between 25 and 200 mm. The lethal limit of plant life in the interior plains coincides roughly with the 75–100 mm. isohyet. Areas situated beyond the above lines do not support vegetation of any kind except under special edaphical or topographical conditions (depressions, wadis, high ground-water table, etc.).

Each of the above climatic variants is confined to a definite zone roughly corresponding to one of the three plant geographical territories into which Palestine is subdivided. Temperature and other climatic factors are rather overshadowed by the moisture factor, which as a minimum factor plays a decisive part on plant life.

The three hydrothermic figures recorded below may serve to illustrate the climatic conditions prevailing in each of the climatic and plant geographical territories of Palestine (Fig. 1).

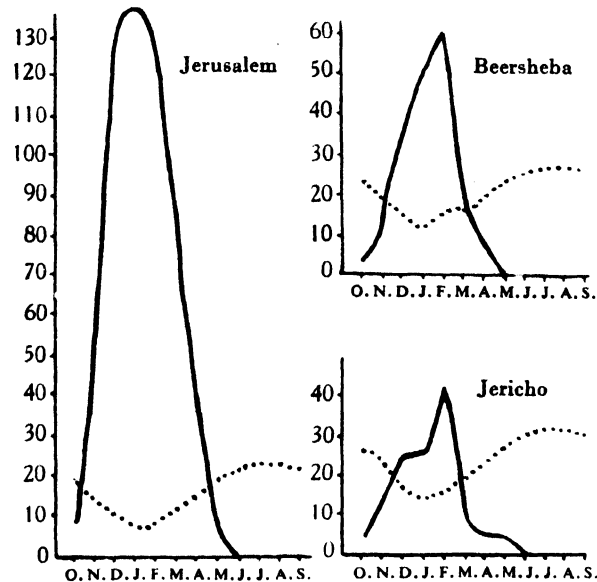


Fig. 1. Hydrothermic graphs of three localities in Palestine: Jerusalem (representing eu-Mediterranean climate), Beersheba (representing steppe or Irano-Turanian climate), Jericho (representing desert or Saharo-Sindian climate). Figures show precipitation in mm. and temperature in °C.

For further information on the climate of Palestine the reader is referred to Ashbel (1938, 1940*a, b*, 1935–43).

#### IV. SOILS

Within the above-mentioned climatic zones the soil factor plays a prominent role in constitution and distribution of plant communities. Edaphical approach to the study of the richly differentiated vegetation within climatically uniform zones has proved indispensable. As this approach has also been a basis for delimitation of the vegetation areas, some details on soil relations may be given here.

General remarks:

(a) Mature soils with well-developed profiles are rare in our region. The progressive course of soil development is greatly impeded by a series of obstacles connected with



climate (wind, rainstorms, etc.), topography (rough orographical features) and man (devastation of natural vegetation), accelerating soil erosion in the mountain region and leading to perpetual rejuvenation of soil profile in lowlands.

(b) Although the mode of soil formation and the constitution of the soil itself is largely determined by the climatical character of the region, there is a series of pedological units in which climate did not obliterate these soil peculiarities, rooted in its lithological origin. One therefore encounters in Palestine different soil varieties side by side within climatically uniform regions. A geological approach to the study of Palestine soils is thus of utmost importance.

(c) Ecological observations in the arid region of Palestine during recent years have revealed that among the edaphic factors affecting physiognomy and constitution of vegetation the highest significance must be ascribed to those chemical and physico-chemical properties which determine water relations and accumulation of injurious salts in the soil.

From the geobotanical point of view the soils of Palestine may be subdivided into the following units: (1) calcareous soils, (2) basalt soils, (3) sandy and sandy-calcareous soils, (4) loess, (5) alluvial soils and (6) saline soils.

#### *A. Calcareous soils*

Within this series the following types may be mentioned:

(1) *Terra rossa*. It is most abundant in and characteristic of the Mediterranean territory. It is derived from hard limestone and dolomites of the Upper Cretaceous and Eocene formations. Its content in humus is rather small.  $\text{CaCO}_3$  ranges generally between 5 and 20%; the silt-clay fraction varies between 20 and 50%. It is the most productive among the soil varieties of the mountain region.

(2) *Whitish grey soils*. These are mainly steppe and desert soils but occur also in the Mediterranean territory. This type is derived from highly calcareous soft marls, chalks and limestones of the aforementioned formations. Its content of  $\text{CaCO}_3$  reaches 50–80%; it is very feebly retentive of moisture and poor in colloidal fractions and sesquioxides. Some of the common varieties may be mentioned here:

(a) Mediterranean whitish grey soil. It occurs side by side with terra rossa, and there is a striking difference in vegetation between these two soil kinds, despite uniformity of climate.

(b) Rendzina soil with a thick layer of humous matter overlaying a highly calcareous grey horizon. It is mainly limited to northern Palestine (Samaria and Lower Galilee).

(c) Steppe and desert soils comprising (1) white calcareous and gypseous Lissan Marls of the Jordan-Araba Valley, (2) immense plains of the interior gravelly deserts (Hammada), (3) rocky steppe and desert soil, (4) highly gypseous hills of the Judean Desert.

#### *B. Basalt soils*

These are confined to the north-east part of the country (Upper Jordan Valley, eastern escarpments of Lower Galilee and north-west Transjordan) and are readily distinguished from terra rossa by the high percentage of silt and clay. They are fairly productive soils when in plains and valleys and rather unfavourable for arboreal vegetation when in oropaedic stage.

### C. *Sandy and sandy-calcareous soils*

These comprise a number of light soil varieties confined to the Coastal Plain and to southern Palestine. Most are eolian in formation. The following varieties are mentioned here:

(1) *Coastal sand dunes*. They occupy a considerable strip along the Mediterranean coast and generally bear little vegetation except in the northern part, where arboreal climax vegetation covers considerable stretches.

(2) *Kurkar soil*. This is derived from calcareous-sandstone hills more or less parallel to the coastal sand-dune ridges. These hills are considered older dunes diagonetically hardened and cemented by solution of lime. They generally overlie a thick layer of a compact brown sandy loam. The kurkar sandstone appears either as friable concretions or as consolidated rocks weathering into a coarse, loose, highly calcareous sand or into a sandy clay.

(3) *Red sand (sandy clay)*. It covers vast stretches of the Sharon Plain and northern Philistaea. It is almost entirely devoid of lime; the parent material is the loam underlying the kurkar cover. It is the most characteristic soil of the citrus region in Palestine.

(4) *Desert sand dunes and sand plains*. These sands are derived either from Nubian Sandstone (Lower Cretaceous) or from igneous rocks (south-east Transjordan and Wadi Araba). Sandy plains bear as a rule more vegetation than other desert types. Even a superficial sand cover overlying desert soil increases the moisture absorption capacity and protects the subsoil against evaporation.

### D. *Loess*

Loess covers a vast area of southern Palestine especially in the Beersheba-Gaza district. It is of eolian origin and consists mainly of desert dust and sand transported by the wind from bare and uncolonised soils to a region of higher precipitation and denser vegetation. It is a fine-grained soil with a medium ration of lime, clay and silt and a high proportion of fine sand. Owing to its physical properties loess represents the most favourable substrate among the steppe soils. It is highly appreciated by the inhabitants, despite being situated in a region of comparatively low rainfall. Winter and very often also summer crops are extensively cultivated on this soil.

### E. *Alluvial soils*

These comprise both transported heavy soils of the great plains and valleys and hydropaedic soils at and near the water bodies. The former consists of red to dark brown-greyish loams highly retentive of moisture and rich in colloidal clay. Where drainage is impeded the tendency towards salinity is marked. The percentage of lime varies generally with the distance from the adjacent mountains from which they are derived. Natural vegetation is generally lacking, due to antiquity of agriculture. Apart from minor areas within the Mountain Region it covers vast expanses in the Philistaea Plain, Acre Plain, Esdraelon Plain, Upper Jordan Valley, etc.

The hydropaedic lands are very characteristic of the Coastal Plain mainly at the outlet region of the latitudinal water courses. A series of swamps have existed here until recently. Another centre of hydropaedic soils is located in the Jordan Valley. One of the greatest swamps of this area is the peat bog of Huleh noted for its papyrus stands.

Another feature of the Jordan Valley and the Dead Sea basin are the Sudano-Deccanian oases, the soil of which is permanently fed by fresh-water sources.

#### F. *Saline soils*

A remarkable part of the Palestine soils belongs to this series. By far the greatest part of them is limited to the Lower Jordan Valley, the shores of the Dead Sea and Wadi Araba. They are chiefly solontchaks (white alkali), the dominating salt being sodium chloride. Pedogenetically they may be subdivided into automorphous and hydromorphous salines. The former are not or only slightly affected by hydropaedic factors. Such are, for example, the Lissan Marls of the higher Jordan terrace north of the Dead Sea and Mount Sodom. Among the hydromorphic salines two varieties are distinguishable in ecology: (a) flooded salines (Wadi Araba, shores of the Dead Sea, etc.) and (b) ground-water salines, i.e. marshes the salinity of which is caused by elevation of the ground-water table (Lower Jordan Valley, etc.).

#### V. PHYTOGEOGRAPHICAL RELATIONS OF THE FLORA

An analysis of the Palestine flora carried out by Eig (1931) revealed that of the 2172 species known at that time from Palestine 826 are Mediterranean, 255 Irano-Turanian, 298 Saharo-Sindian, 15 Eurosibero-Boreoamerican and 39 Sudano-Deccanian. The balance, 739 species, are bi- or pluriregional. Of these species 370 are Mediterranean—Irano-Turanian, 11 Mediterranean—Saharo-Sindian, 47 Saharo-Sindo—Irano-Turanian, 12 Mediterranean—Irano-Turanian—Saharo-Sindian, 104 Eurosibero-Boreoamerican—Mediterranean—Irano-Turanian, 31 Saharo-Sindo—Sudano-Deccanian, while 164 belong to tropical, subtropical and boreo-tropical groups. Among the Mediterranean element 319 (39%) are omni-Mediterranean, 446 (54%) east Mediterranean, 14 west Mediterranean, 33 north Mediterranean and 14 south Mediterranean. The Saharo-Sindian element consists mainly of west and middle Saharo-Sindian species, while the Irano-Turanian element consists chiefly of Mauritanian steppe, Mesopotamian and Irano-Anatolian species. The number of endemic species recorded by Eig from Palestine amounts to 115.

Since the above analysis, over 200 species have been added to the flora of Palestine, many of them new to science. But with the exception of the endemics the ratio of the various plant geographical groups will scarcely be altered by this addition.

#### VI. PHYTOGEOGRAPHICAL SUBDIVISION OF PALESTINE

In its geographical position Palestine constitutes a meeting ground for three great plant-geographical regions, viz. the Mediterranean, the Irano-Turanian and the Saharo-Sindian. Eig (1931, 1938) was the first to fix more or less accurate boundaries for these three regions in Palestine and to subdivide Palestine into Mediterranean, Irano-Turanian and Saharo-Sindian territories, each of which is characterized by special flora and vegetation. The Sudano-Deccanian and Eurosibero-Boreoamerican elements do not occupy particular territorial units. While the former is limited mainly to moist habitats of the Saharo-Sindian territory, the Eurosibero-Boreoamerican element is scattered here and there mainly in hydrophytic habitats.

The Mediterranean territory is the district of arboreal climax communities. Owing to the vicinity of the desert as well as to certain historical circumstances Palestine's wood

flora has been subjected rather more than elsewhere in the Mediterranean to heavy destruction, so that at present shrub formations (Batha and Garigue) constituting permanent stages of developmental seres cover the greater part of this territory.

The Irano-Turanian territory is steppe country devoid of arboreal climax except in the northern and western parts, where associations of *Pistacia atlanticae* and *Zizyphion Loti* occur. Agriculture is unstable here for the most part due to scant and irregular rain. There are, however, immense stretches of loess and sand-loess soils which support a kind of 'steppe agriculture'. Vegetation is mostly single-layered, but comparatively rich in species.

The Saharo-Sindian territory is the most barren part of the country. No arboreal vegetation is encountered except in oases, salines and near water bodies. Vegetation cover is very thin, and there are some areas almost completely devoid of vegetation. Salt lands, sand dunes and hammadas are most characteristic of this territory.

## VII. VEGETATION

A brief description of the main types of vegetation presented in the accompanying map is given below. For the sake of completeness mention is made also of the vegetation of Transjordan and the Far Negeb, which are not included in the map. As stated, this enumeration is not exhaustive and the denomination of some of the units recorded below may perhaps be altered in future studies.

### A. Mediterranean forests and Maquis

(1) *Pinion halepensis*. This type of forest occurs in Palestine mostly as remnants and small stands in the higher zone of the mountains. One of the most typical associations is the *Pinus halepensis-Hypericum serpyllifolium* association (Eig, 1938). Among the important stations of this forest the following localities may be mentioned: Mt Carmel, Yerka (Galilee), environs of Um Safah (Samaria), environs of Hebron (Judean Mountains) and Gilead (Transjordan).

In its composition it is a mixed forest containing a considerable number of associates characteristic of other Mediterranean arboreal associations, e.g. *Quercus calliprinos*, *Arbutus andrachne*, *Phyllirea media*, *Pistacia lentiscus*, *Pistacia palaestina*, *Genista sphacellata*, etc. It cannot be decided at the moment whether this composition is primary or the result of clearing. Syngenetically it is a climax association of certain habitats of the mountains developing through a number of seral stages, e.g. Batha and Garigue associations.

Ecologically this pine forest is mostly confined to highly calcareous grey soils derived mainly from soft rocks of the Upper Cretaceous and Eocene. This soil is considerably poorer in nutrient matter and moisture than terra rossa. It ascends the mountains to 1000 m. altitude.

Of value as timber and incapable of regeneration upon destruction by axe or fire, it must have disappeared since from several parts of the country. Recently extensive reafforestation of *Pinus halepensis* has been carried out by the Government and the Jewish National Fund.

In Syria this association is replaced by *Pinetum brutiae*, very abundant there in the northern part of the coastal region.

(2) *Quercion ithaburensis*. Of this type at least three associations are to be distinguished, each confined to a particular district and to special ecological conditions as follows:

(a) *Quercus ithaburensis-Styrax officinalis* association containing, apart from the two leading species, a series of other shrubs and trees of Maquis and Garigue, e.g. *Pistacia palaestina*, *Crataegus azarolus*, *Ceratonia siliqua*, *Phyllirea media*, *Cercis siliquastrum*, *Quercus calliprinos*, *Phlomis viscosa*, *Cistus salviaefolius*, *Calycotome villosa* and others. It is confined mainly to grey soils of the rendzina type in the Ephraim Mountains and the western hill region of Lower Galilee. It does not ascend the mountains beyond 500 m. and it avoids typical Mediterranean exposure. From its distribution in Palestine one could conclude that this forest is to a certain extent 'pushed' to habitats not suited to other Mediterranean forest or Maquis vegetation. In the past this association no doubt inhabited large areas of the Esdraelon Plain now under extensive agriculture (Eig, 1933). In the above-mentioned districts it is a climax association; the earlier stages of the seres leading to this climax are more or less similar to those of *Quercus calliprinos-Pistacia palaestina* association.

(b) *Quercetum ithaburensis arenarium*. Although at present very fragmentary, this association formerly occupied a considerable and continuous area of the Sharon Plain. This is obvious not only from the remnants existing to-day but also from historical records (Eig, 1933). Observation leads to the conclusion that this forest has formed stands with a rather poor intermixture of other Mediterranean trees or shrubs. At present remnants of this forest are scattered in the Sharon over large plains of red sand (sandy clay) covered by the *Eragrostis bipinnata-Centaurea procurrens* association which, according to Eig (1939), is no doubt one of the most permanent successional stages leading here to the *Quercetum*.

(c) *Quercus ithaburensis-Pistacia atlantica* association. This association is well represented in the western escarpments of the Golan and Gilead (Transjordan) facing the Huleh and Upper Jordan Valley. It is confined here to lower altitudes and to areas situated near the Mediterranean-Irano-Turanian boundary. *Pistacia atlantica*, an Irano-Turanian tree, is richly represented in this association. Further details on composition, ecology and syngensis of this forest are not known to us.

(3) *Quercion calliprini*. This is the most important group of arboreal associations within Mediterranean Palestine. In its physiognomy and composition it constitutes the most characteristic type of the East Mediterranean Maquis. At least three well-defined plant associations are included within this alliance.

(a) *Quercus calliprinos-Pistacia palaestina* association (Eig, 1927, 1938). This is the most abundant association of the Maquis. A distinction may be made between the typical and the 'mesophyllous' variety confined to the shady northern or western slopes of the mountains. The typical form contains, apart from *Quercus* and *Pistacia*, *Crataegus azarolus*, *Phyllirea media*, *Styrax officinalis*, *Rhamnus palaestina*, *Pistacia lentiscus*, *Ceratonia siliqua*, *Arbutus andrachne*, etc., while the mesophyllous variety harbours, in addition to the above-mentioned shrubs and trees, *Laurus nobilis*, *Cercis siliquastrum*, *Rhamnus alaternus* and sometimes also *Acer syriacum*. Both include, apart from the trees and shrubs mentioned above, a series of Garigue and Batha shrubs such as *Calycotome villosa*, *Salvia triloba*, *Cistus villosus*, *C. salviaefolius*, *Satureja thymbra*, *Spartium junceum*, *Poterium spinosum*, etc. The coverage may reach 100% in places not affected by man.

More or less well-preserved areas of this association are found in Upper Galilee,

Mt Carmel, Gilead and Samaria, but elsewhere it has suffered seriously from destruction. Immense areas in the mountains exhibit only scant remnants of this Maquis type or are entirely deforested.

The question whether the Maquis represent the final stage of the successional sere (climax) within the Mediterranean region has since been subject to discussion not only in regard to Palestine but also to other Mediterranean countries. Much evidence recently collected gives rise to the opinion that this type of Maqui is capable, when protected against human interference, of development into forests. It should be mentioned here that the main woody components of the Maqui may assume the form of trees. Single aged trees and remnants of forest are to be found in Arab cemeteries where they are secured by tradition against destruction.

The successional sere leading to either Maquis or forests of *Quercus-Pistacia* starts from a series of initial plant communities and passes mostly through *Poterietum spinosi* and *Cistetum*, *Calycotometum* or other associations of Batha and Garigue (depending mainly upon the edaphic environment). These shrub or dwarf-shrub associations are not only important and permanent stages in the progressive course of the sere but also play an important part in the retrogressive course of the sere caused through destruction of the arboreal associates by man. Typical Mediterranean Batha and Garigue associations may thus be regarded mostly as early or derivative stages of the sere leading towards Maqui and forest climax.

Ecologically the *Quercus calliprinos-Pistacia palaestina* association requires typical Mediterranean conditions both climatically and edaphically. Terra rossa and to a less extent grey-brown calcareous soil are found under this association. It is generally limited to between 200 and 1200 m. above sea-level and to precipitation not below 400 mm. in quantity.

(b) *Ceratonia siliqua-Pistacia lentiscus* association (Eig, 1939). This association resembles the *Oleeto-Lentiscetum* characteristic of some west Mediterranean countries. It is limited to western Palestine and is entirely absent in Transjordan (Feinbrun & Zohary, 1942).

This association is very peculiar physiognomically because of the more or less continuous coverage of shrubs and the scattered trees of *Ceratonia siliqua*. Among the shrubs associating with *Pistacia lentiscus* the following are common: *Calycotome villosa*, *Cistus salviaefolius*, *C. villosus*, *Phlomis viscosa*, *Oryzopsis miliacea*, *Asparagus aphyllus* and other species of the Garigue and Batha associations. Occasionally *Pistacia* may reach the size of a small tree when protected against cattle.

While closely confined to typical Mediterranean climate it exhibits a wider range of edaphical requirements, and it is according to this factor that this association may be subdivided into at least three variants: the mountainous, the coastal sandstone (kurkar) and the sand dune.

This association does not rise above 400 m. above sea-level, except along the eastern edge of the mountain region where there is no competition with the *Quercus calliprinos-Pistacia palaestina* association.

It is worthy of mention that on terra rossa and grey Mediterranean soil this association advances to the south approximately as far as the latitude of Gaza, whereas on Kurkar sandstone it stops near Caesarea, and on the coastal sand dunes its southern limit passes near Nathania. In the latter habitat it is a climax association of a psammosere of which *Artemisietum monospermae* constitutes one of its permanent stages.

(c) *Quercus calliprinos-Juniperus phoenicea* association (Feinbrun & Zohary, 1942). It is confined to the mountains of Edom (southern Transjordan) in the region of the Nubian sandstone formation. It differs strikingly in composition from the other Maquis associations by harbouring a number of Irano-Turanian shrubs as underwood, not included in the attached map.

Besides these three associations of the Quercion remnants of a semi-steppe, Maqui types are met with in which *Crataegus azarolus* or *Prunus amygdalus* are the only shrubs or trees. They are local and confined to a belt adjacent to the Irano-Turanian border. Nothing can be said about the primary composition of this type which occurs in Transjordan also.

### B. *Mediterranean Garigue*

In Palestine Garigue (Mediterranean shrub and semi-shrub vegetation) is less common than Batha (see below). It is represented here by some more or less well-marked plant associations which may tentatively be grouped in the following alliances:

(1) *Cistion villosae*. This comprises the *Cistus villosus-Cistus salviaefolius* association and its variants, *Salvietum trilobae* (Eig, 1927, 1938), *Saturejetum thymbrae*, etc. The most important constituents of the Cistetum may be mentioned here: *Cistus villosus*, *C. salviaefolius*, *Teucrium creticum*, *Origanum syriacum*, *Helichrysum sanguineum*, *Thymbra spicata*, *Serratula cerinthifolia*, *Oryzopsis miliacea*, *Stipa aristella*, *Ruta graveolens*, *Nepeta curviflora*, *Calycotome villosa* and a great number of annuals. The above-mentioned associations constitute mostly either permanent stages of the successional sere leading to or retrogressive stages derived from various Maquis and forest associations. One often finds transitional stages between Garigue and Maquis.

(2) *Calycotomion villosae* consists of at least three associations as yet inadequately studied: one a typical Mediterranean strictly limited to the mountain region. Here the dominant *Calycotome* is associated with plants characteristic of *Poterietum* and *Cistetum*. The second association is confined to the kurkar hills and sandy loams of the Coastal Plain. A series of psammophytes are often associated here with the dominating *Calycotome*. The third association is confined to the eastern and southern edges of Mediterranean territory where semi-steppe Batha associations dominate and where *Calycotome* is accompanied by a series of plants typical of Mediterranean—Irano-Turanian borderland. While the typical *Calycotometum* is always one of the seral associations leading to Maquis and forest, the coastal and the semi-steppe *Calycotometum* may constitute the final association of certain seres (Eig, 1935).

### C. *Mediterranean Batha*

The Hebrew name Batha was given by Eig (1927) to Mediterranean dwarf shrub formations common and characteristic of the east Mediterranean countries. The following groups of associations have tentatively been distinguished within this type of vegetation:

(1) *Poterion spinosi*. This consists of three well-marked associations: *Poterietum spinosi typicum*, *Poterieto-Thymelaeetum* and *Poterietum spinosi semistepposum*.

(a) The typical *Poterietum* is confined to eu-Mediterranean conditions of the mountain region. Its most characteristic components are *Poterium spinosum*, *Teucrium polium*,

*T. divaricatum*, *Carlina involucrata*, *Pallenis spinosa*, *Thrincia tuberosa*, *Bellis silvestris*, *Orchis anatolica*, *O. papilionacea*, *Anemone coronaria*, *Ranunculus asiaticus*, *Allium stamineum*, *Dactylis glomerata*, *Salvia judaica*, *Helichrysum sanguineum*, *Origanum syriacum* and a long series of geophytes and annuals. Although this *Poterietum* is a well-defined association designated by the wide dominance of *Poterium*, there occur transitions between it and some associations of the more advanced stages of the sere (Garigue) on the one hand and between it and earlier stages (initial and segetal associations). Some variants are accordingly to be distinguished in this association.

The typical *Poterietum* is the predominant association of the terra rossa region. It occurs, however, in the grey-brown soil of the south-west hill region also. It requires more or less deep soil, ascends the mountains to 1200 m. in height and often exhibits high coverage.

Syngenetically it is a permanent stage of certain progressive seres leading to arboreal and arborescent climaxes of the Mediterranean territory. It is also a degradation stage resulting from devastation of Maqui and Garigue.

(b) *Poterieto-Thymelaeetum*. This is confined to the kurkar sandstone hills of the Coastal Plain. *Thymelaea hirsuta* is codominant and sometimes also the leading species of the association. It often contains some Irano-Turanian species and Mediterranean psammophytes, for instance *Gypsophila rokejeka*, *Heliotropium rotundifolium*, *Scabiosa ucranica*, *Tulipa saronensis*, *Scabiosa rhizantha*, etc.

(c) *Poterietum spinosi semistepposum*. This is limited to the Mediterraneo—Irano-Turanian borderland, but also occurs frequently on white greyish highly calcareous soil in the midst of Mediterranean territory. Apart from the dominating *Poterium*, it includes a series of species characteristic of the semi-steppe Batha to be dealt with below. Such plants are, for instance: *Anchusa strigosa*, *Echium angustifolium*, *Alkanna strigosa*, *Heliotropium rotundifolium*, *Ballota undulata*, *Ononis natrix*, *Echinops blanchena*, *Erysimum crassipes*, *Carlina corymbosa*, *Linaria aegyptiaca*, *Noëa mucronata*, etc. In extreme conditions this association may be regarded as a climax vegetation.

(2) *Thymion capitati*. Two associations are well distinguished, one the mountainous *Thymetum* and the other the *Thymus capitatus-Andropogon hirtus* association (Eig, 1939). The former replaces the *Poterietum* on stony or marly ground and never occupies wide continuous areas. *Thymus* is often associated here with *Fumana thymifolia*, *Micromeria nervosa*, *Phagnalon rupestre* and many others.

The *Thymus capitatus-Andropogon hirtus* association is widely distributed over the kurkar hills of the Coastal Plain and often contains a series of plants of sandy habitats. While the mountain *Thymetum* shows a clear position within the seres leading to Garigue and Maquis, no data have been collected on the syngenetical relations of the *Thymus-Andropogon* association.

(3) *Varthemion iphionoidis*. This group of associations is limited to rocky habitats within the Mediterranean territory. The most common plant association is of *Varthemia iphionoides* and *Stachys palaestina* which occurs all over the mountain region of Palestine in a series of variants. Apart from *Varthemia* and *Stachys* this association harbours a few other characteristic plants such as *Ballota saxatilis*, *Micromeria serpyllifolia*, *Podonosma syriaca*. Mention should also be made of *Umbilicetum intermediae*, which inhabits crevices of shady rocks of stone walls, *Hyosciametum aurei*, *Pennisetetum asperifoliae* and others.



*D. Mediterranean semi-steppe Batha*

Under this heading we include tentatively a series of associations of notably hemi-cryptophytic plants which occur within a belt bordering the Irano-Turanian territory. They are as yet inadequately studied, but some of them are well marked in physiognomy, composition and ecology. Whitish grey calcareous soils on the eastern and southern escarpments of the mountain belt and rainfall not exceeding 350 mm. per annum are the typical conditions to which this vegetation is bound. Some of them may be mentioned here.

*Salvia graveolens-Ballota undulata* association. Very abundant in the whitish grey calcareous soils of Moab and Edom (Transjordan) and less common in the northern boundary of the Negeb and near the western limit of the Judaeian Wilderness. Among the perennials associated with the two codominants the following are phytosociologically most important: *Ononis natrix*, *Anchusa strigosa*, *Eryngium glomeratum*, *Onopordon palaestinum*, *Echinops blanchena*, *Carlina corymbosa*, *Scrophularia xanthoglossa*, *Noëa mucronata*, etc. Despite the presence of some Irano-Turanian components this association is still Mediterranean, and there are evidences that a kind of *Crataegum azaroli* or *Prunetum amygdali*, the fragments of which are often met with in the region of this association, may be regarded as a hypothetical climax here.

Of the other associations of this semi-steppe Batha the *Ononidetum natrixis* is common on grey-whitish soils, the *Convolvulus dorycnium-Carlina corymbosa* association is most characteristic of the basalt area especially at its eastern edge. Similarly the *Psoralea bituminosa-Echinops blanchena* community is confined to the Eocene hard limestone slopes of the Canaan Mountains facing the Upper Jordan Valley.

*E. Mediterranean psammophytic vegetation*

Apart from the plant associations mentioned above in connexion with forest, Maquis, Garigue and Batha, the Coastal Plain of Palestine harbours a series of psammophytic plant communities not occurring elsewhere in the Mediterranean territory of the country. The occurrence of particular edaphic conditions (sand dunes, sandstone hills, red sands, i.e. sandy clay soil) accounts not only for the penetration of many Saharo-Sindian and Irano-Turanian plants into this region, but also for the predominance of some of those plants within certain associations, despite the typical Mediterranean climate of this plain. The plant communities recorded here have been studied mostly by Eig (1939).

(1) *Artemision monospermae*. This group is confined to the sand-dune belt of the coast and consists of:

(a) *Ammophila arenaria-Cyperus conglomeratus* association (shifting sand dunes).

(b) *Artemisia monosperma-Cyperus mucronatus* association with its variants includes some phytosociologically important perennials such as *Polygonum equisetiforme* var. *arenarium*, *Panicum turgidum*, *Retama roetam*, *Silene succulenta*, *Medicago marina* and a series of annuals. In the northern part of the Coastal Plain it constitutes, as already mentioned, a permanent stage of a psammosere leading to the *Ceratonia siliqua-Pistacia lentiscus* climax.

(c) *Tamaricetum pseudo-pallasii* (permanent dunes of the Gaza district).

(d) *Lithospermum callosum-Scrophularia hypericifolia* (troughs between dunes and sandy plains).

(2) *Lotus creticae*. This is limited mainly to the high coast and its escarpments on sandy clay or Kurkar sandstone. Most important are *Lotus creticus* and *Sporobolus arenarius*. The two dominants are frequently associated with *Agropyrum junceum*, *Pancratium maritimum*, *Euphorbia paralias*, *Plantago sarcophylla*, *Senecio joppensis*, *Glaucium flavum*, *Cakile maritima*, *Trisetum koelerioides*, *Orlaya maritima*, etc.

(3) *Eragrostion bipinnatae*. This consists mainly of the following associations:

(a) The *Eragrostis bipinnata*-*Centaurea procurrens* association, is, in appearance, strongly reminiscent of grass steppe. It is confined to red sand (sandy clay) almost or entirely deprived of lime. Although situated in the midst of a Mediterranean climate the dominant species of the association (*Eragrostis*) is Saharo-Sindian in origin. It is very rich in species and displays high coverage. The following species are the most characteristic of this association: *Aegilops longissima*, *A. sharonensis*, *Tulipa sharonensis*, *Corynephorus articulatus*, *Nigella arvensis*, *Reseda orientalis*, *Anchusa aggregata*, *Crepis aculeata*, *Daucus littoralis*, *Trifolium dichroanthum*, *T. stenophyllum*, *Muscari maritima*, *Lupinus termis*, *L. palaestinus*, *L. hirsutus*, *L. angustifolius*, *Trigonella cylindracea*, *Maresia pulchella*, etc.

This association occupies the greater part of the Sharon Plain and serves as the best indicator of 'citrus soil' in Palestine. Two Sudano-Deccanian trees are scattered here and there in the region of this association: *Zizyphus spina-christi* and *Ficus sycomorus*. They are of no syngenetical significance here. The climax association of this area (north of the Yarkon River) is a kind of Quercetum ithaburensis already mentioned above.

(b) *Ormenidetum mixtae*. It is one of the most common initial stages of the sere leading to the *Eragrostis*-*Centaurea* association.

(c) *Helianthemum ellipticae*. This association is confined to Kurkar hills (south of the Yarkon River). *Helianthemum* is mostly associated with *Retama roetam*, *Gypsophila rokejeka*, *Thymelaea hirsuta*, *Aristida sieberiana*, *Argyrolobium uniflorum*, *Scabiosa ucranica*, *Echium angustifolium*, *Salvia lanigera*, etc. Despite the Mediterranean climate most of the associates are desert or steppe plants.

#### F. Irano-Turanian vegetation

The vegetation of the Irano-Turanian territory is less known than that of the Mediterranean. Here no arboreal vegetation occurs except in the Upper Jordan Valley or in other ecologically favourable districts. The plant communities are mostly open. There is generally no successional development or physiognomical differentiation (stratification) of the plant communities. The following groups of associations may be distinguished here:

(1) *Pistacion atlanticae*. Only single trees or small forest remnants are encountered in Cisjordan, mainly near the Mediterraneo—Irano-Turanian border line, and on higher elevations of the Far Negeb, but there are extensive forests of it in the northern part of the Syrian Desert and smaller stands in Transjordan (Zohary, 1940c). In the accompanying map this could not be indicated.

(2) *Zizyphion loti*. It occupies wide stretches in Palestine of the basalt area and the calcareous soil of the Middle and Upper Jordan Valley. A series of associations of this union may be distinguished. For the time being two of them may be mentioned: (a) *Zizyphetum loti* of the Middle Jordan Valley and the *Zizyphus lotus*-*Zizyphus spina-christi* community of the Beisan Valley and the Ginosar Plain. The latter is confined to irrigated soils where the destroyed shrubs of *Zizyphus lotus* are replaced by *Zizyphus spina-christi*. The primary centre of both of the above-mentioned associations is no doubt

the Middle and Upper Jordan Valley, where the annual precipitation does not exceed 300 mm. and the temperature minima are less extreme than in the adjacent mountains. From this centre *Zizyphetum loti* presumably spread into the adjacent basalt area of Lower Galilee where it constitutes a secondary climax. At present both associations are limited to an altitude ranging between  $-200$  and  $+200$  m.

(3) *Retamion duriaei*. It is one of the outstanding fruticeta of the rocky escarpments facing the Jordan Valley both in Cis- and Transjordan. According to exposure, altitude and rock constitution several units will no doubt be distinguished in future. As yet few observations have been made on the *Retama-Phlomis brachyodon* association and the *Retama-Rhus tripartita* association (Eig, 1938).

(4) *Artemision herbae-albae*. Into this group we include tentatively a series of dwarf shrub steppe associations, occupying a considerable belt in the Judaeen Desert, the Near Negeb and Transjordan. The most important and well-defined units are *Artemisietum herbae-albae* and its variants, *Noëetum mucronatae*, *Salsoletum villosae*, *Haloxylonetum articulati*, *Phlomidetum brachyodontis*, *Astragaletum forskahlei*. These are confined to typical immature grey steppe soil (*Noëetum*, *Artemisietum*, *Salsoletum*, *Astragaletum*), to loess (*Artemisietum*, *Haloxylonetum*) or to soil patches between flat hard rocks (*Phlomidetum*). Coverage may reach 50–80% here.

In the attached map it was impossible to separate the above-mentioned groups of associations from one another. On the other hand, the area designated by a particular variant of *Artemisietum herbae-albae* which constitutes the climax of the loess region of the Negeb was separated from this and marked particularly. This area is occupied by three segetal associations of the *Achilleion santolinae* to be mentioned below.

#### G. Saharo-Sindian vegetation

Structurally this vegetation is designated by communities consisting of only a single or a few perennial species. They display very feeble coverage, often not in excess of 10%. The following main groups have been differentiated (compare Eig, 1935, 1938).

(1) *Zygophyllion dumosi*. This group is confined to rough stony hillsides covered with boulders and coarse gravel. Only a very scant amount of highly calcareous soil is accumulated between the stones. Of the three associations known to us from these habitats, viz. *Zygophylletum dumosi*, *Gymnocarpetum fruticosi* and *Reaumurietum palaestinae*, the first is the most common. The following species have been noted as frequent associates of *Zygophyllum dumosum*: *Haplophyllum tuberculosum*, *Halogeton alopecuroides*, *Reaumuria palaestina*, *Linaria haelava*, *Atriplex parvifolia*, *Reseda muricata*, *Gymnocarpus fruticosus*, *Salsola inermis*, *Statice thouini*, *Stipa tortilis*, and *Anabasis articulata*. This association occurs both in the Judaeen Desert and in the Negeb of Palestine. It is rather rich in species.

(2) *Suaedion asphalticae*. This is chiefly confined to highly gypseous hillsides of the Judaeen Desert. *Suaedetum asphalticae* and *Chenoleetum arabicae* are the two associations known to us hitherto. *Suaedetum* is endemic in Palestine and is limited to an altitude ranging between  $-300$  m. to approximately  $+50$  m. above sea-level. The main plants noted of this association were *Suaeda asphaltica*, *Poa eigii*, *Reboudia pinnata*, *Leptaleum filiforme*, *Plantago coronopus* var. *crassipes*, *P. ovata*, *Senecio coronopifolius*, *Allium hierochuntinum* and *Stipa tortilis*.

(3) *Anabasis articulata*. This is the most characteristic plant group of the vast Hammada tracts of the Negeb and Transjordan. These gravel plains are very sparsely vegetated, and plant growth is chiefly limited to depressions. Of the plant associations to be included within this group three may be mentioned here: *Anabasetum articulatae*, *Zilletum spinosi* and *Zilla spinosa*-*Noëa mucronata*. No detailed data are available in regard to the particular ecological requirements of these associations. *Anabasetum* is most abundant and most characteristic of the deserts of Palestine and the neighbouring countries. Its coverage often does not exceed 1%, frequently it is *Anabasis* itself, which forms pure stands (Zohary, 1944b).

(4) *Haloxylon salicornici*. This is confined to sand dunes and sandy plains and valleys (Wadi Araba, southern Negeb, etc.) of the granite and Nubian sandstone region. While *Haloxylonetum salicornici* is an association of low shrubs known from Sinai, Iraq, Wadi Araba and the Negeb, *Haloxylonetum persici* forms in Wadi Araba and probably also in the Arabian Nefud extensive 'Saxaul forests' (Zohary, 1940a, 1944b). The relations between these two associations are not as yet clear.

(5) *Aristidion scopariae*. The sand dunes and sandy plains of the interior deserts bear vegetation differing from that of the Mediterranean coastal dunes, although desert psammophytes may penetrate into the Coastal Plain and play a rather important part in the vegetation there. Of the plant associations observed (though not sufficiently studied) mention may be made of *Aristidetum scopariae* (semi-stable dunes), *Retametum roetami arenarium* (valleys between dunes and sandy hillocks), and *Artemisietum monospermae* and its variants. One of these variants covers (in the southern part of the country) a considerable tract of sandy ground overlaying a loessy subsoil. *Artemisia* is here very sparse, but its annual associates, notably *Aegilops bicornis* or *Lolium multiflorum*, or both together, form dense stands of grass steppe appearance.

The above-mentioned plant communities far from exhaust the desert vegetation. Among others there is a series of plant associations very characteristic of stony or sandy wadis, such as stands of *Retama*, *Tamarix-Calligonum comosum* association, fragments of various *Tamariceta*, *Acacietum*, etc. Sufficient data are not available concerning this vegetation.

#### H. Sudano-Deccanian vegetation

As already mentioned, Palestine harbours thirty-nine Sudano-Deccanian species, a large part of which are shrubs and trees. Vegetationally these plants constitute a few associations which could be classed under *Zizyphion spina-christi*. This group of units is mainly limited to the oases around the Dead Sea and along the Lower Jordan Valley. While most associations are fragmentary and therefore ill-defined, the *Zizyphus spina-christi-Balanites aegyptiaca* is most strikingly abundant, and well-marked phytosociologically. Among the constituents other than *Zizyphus* and *Balanites* the following may be mentioned: *Callotropis procera*, *Solanum incanum*, *Acacia tortilis*, etc. In the southern part of the Dead Sea there also occur in addition to the above-mentioned species: *Salvadora persica*, *Moringa aptera*, *Cordia gharaf*, and *Maerua crassifolia* within this association.

While in the Lower Jordan Valley *Zizyphus spina-christi* is undoubtedly primary it seems to be secondary in almost all the alluvial plains of Palestine.

It is worthy of mention that remnants of *Acacietum albidae* form pure stands in some localities of Palestine (environs of Beit Jubrin, Nahalal, Wadi Bireh, Wadi Taiba, etc.). Its discontinuous distribution and its occurrence in strikingly diverse habitats point to the assumption that these stands are relics of ancient tropical vegetation which at one time covered various parts of Palestine.

### I. *Halophytic vegetation*

A wide area of the lower Jordan Valley, the Dead Sea shore and Wadi Araba is covered with a rather diversified halophytic vegetation. This vegetation is differentiated into a considerable number of associations conditioned by edaphic factors such as soil texture, moisture content, salt concentration and seasonal movement of salts within the soil. The salt in consideration is mainly sodium chloride. Among the salines of Palestine, at least four well-defined habitats may be distinguished: (1) permanent saline or brackish springs or brooks, (2) salines flooded during the whole or a part of winter, (3) salines with no open-water surface but with a more or less high water table, (4) automorphous salines, i.e. dry desert salines (floors of ancient salt lakes, etc.), the salt of which could not be leached out because of the very scant rainfall of the region. The saline vegetation may be subdivided into four major groups according to these habitats (Zohary & Orshansky, 1942*b*).

(1) *Junceto-Phragmition*. This group characterizes banks of permanent saline or brackish water bodies. Vegetation is zonally arranged along or around the water body. The first zone is generally occupied by a band of *Phragmites communis* forming fairly pure stands. In the second zone *Juncus maritimus* var. *arabicus* forms a broad belt; it is generally associated with *Inula crithmoides*, *Statice limonium*, etc. The third zone is inhabited by *Aeluropus litoralis*. Sometimes a fourth belt is formed by stands of *Tamarix maris-mortui*.

(2) *Tamaricion tetragynae*. It is confined to salines flooded for a certain amount of time. According to percentage of soluble salts, soil texture and amount of moisture the following associations were distinguished: (a) *Tamarix tetragyna-Arthrocnemum glaucum* association and its variants (southern and northern shore of the Dead Sea), (b) *Suaedetum monoicae* (occupying considerable flats in Wadi Araba and the southern Dead Sea Ghor) and *Nitrarietum retusae* (Wadi Araba and Dead Sea Ghor).

(3) *Atripliceto-Suaedion*. This group is very abundant and most characteristic of the great flats formed at the outlet region of the wadis crossing the Lissan Marl plateau between Jericho and the Dead Sea. This region is rarely flooded, but it generally displays a more or less high water table. The following associations have been clearly distinguished here: (a) *Atriplicetum*, *Halimi jordanicum*, (b) *Atriplex halimus-Suaeda fruticosa* association, (c) *Suaedetum palaestinae* and its variants, (d) *Salsoletum rosmarinus*, etc.

(4) *Salsolion tetrandra* (Eig 1938). This group occupies the salty soils of the Lissan Marl formation (dried-out floor of the diluvial so-called 'Jordan Sea'). Two plant associations are characteristic of these habitats: (1) *Salsoletum tetrandrae* and (2) *Salsoletum villosae jordanicum*. *Salsola villosa* exhibits a wide range of ecological requirements; while in the Irano-Turanian territory it forms the above-mentioned *Salsoletum villosae* on grey steppe soils and hillsides, it is here a leading species of a more or less halophytic association.

J. *Hydrophytic vegetation*

Hydrophytic vegetation occurs in Palestine mainly in two centres: (1) The Coastal Plain, which a series of latitudinal watercourses traverse on their way to the Mediterranean Sea. Most of these watercourses are impeded here in drainage because of the dune ridges and kurkar hills arranged in longitudinal rows. This gave rise to the formation of swamps along the northern part of the Coastal Plain and allowed the development of a rich hydrophytic vegetation. (2) The other centre is formed by the Jordan Valley from the sources of the Jordan in the north to the Gulf of Aqaba. The Jordan River and its latitudinal tributaries, the Lake of Huleh and Kinnereth, are the main hydrophytic features of the valley. The following vegetational groups were distinguished among Palestine hydrophytic vegetation:

(1) *Potamion*. It includes the *Nuphareto-Ceratophylletum*, *Potamogetonetum* and *Myriophylletum*. All are well represented especially in the Lake of Huleh.

(2) *Phragmition*. This comprises a series of zonally arranged plant associations on low banks or shores of water bodies. *Phragmites communis-Typha angustata*, *Juncetum acuti*, *Inuletum viscosae* are the main plant associations. Within this alliance the *Cyperetum papyri* of the Huleh swamps is also included.

(3) *Rubion sancti*. This comprises mainly the *Rubus sanctus-Lythrum salicaria* association so characteristic of high river banks and wadis. *Salicetum acmophyllae* is another plant association especially developed on the banks of the Yarkon River.

(4) *Populion euphraticae*. This forest fringes the middle and lower course of the Jordan River. It comprises *Populetum euphraticae*, *Tamaricetum Jordanis*, etc. It is mainly Irano-Turanian or Saharo-Sindian.

(5) *Nerion oleandri*. This inhabits stony, ephemeral or permanent, rivers, especially of the mountain region. It comprises *Nerietum oleandri*, *Nerium oleander-Arundo donax* association on rocky banks or wadi beds, *Viticetum agni-casti* (ephemeral well-watered wadis with gravelly beds), *Platanetum orientalis* (mountain streamways), etc.

There are more units which cannot be mentioned here.

K. *Hemerophytic vegetation*

Segetal and ruderal vegetation are comprised under this heading. We shall, however, deal here only with the segetal vegetation, which occupies in Palestine vast expanses, notably of the Mediterranean territory. The antiquity of agriculture in this country and the total extermination of primary vegetation from a series of alluvial valleys have encouraged the development of a very rich and vegetationally diversified flora of obligatory and facultative weeds. Over 500 species of the Palestine flora are segetal or semi-segetal. A series of plants confined in Palestine and Syria to segetal habitats are still to be found in the adjacent steppe as components of primary associations. Three main habitats are to be distinguished in this connexion: (1) Alluvial plains covered with a deep layer of grey-brown transported soil of heavy texture. This habitat covers the greater part of the arable land of Palestine (Philistea coast, Acre Plain, Esdraelon Plain, Upper Jordan Valley, etc.). (2) Grey or red, often shallow soils of the mountain region never forming large continuous areas. (3) Loess soil of the Beersheba-Gaza district.

Each of these habitats is characterized by a particular well-defined group of vegetation:

(1) *Prosopidion farcatae*. This comprises the segetal vegetation of the alluvial plains.

Among the various phytosociological units the *Prosopis farcata*-*Scolymus maculatus* is most common. Apart from the two leading species the following may be mentioned as associates of the spring aspect: *Ridolfia segetum*, *Saponaria vaccaria*, *Sinapis arvensis*, *Rapistrum rugosum*, *Raphanus raphanistrum*, *Phalaris paradoxa*, *Securigera securidaca*, *Cephalaria syriaca*, *Ammi majus*, *Daucus aureus*, *Euphorbia cybirensis*, *Cachrys goniocarpa*, *Convolvulus arvensis*, *C. hirsutus*, *Teucrium spinosum*, etc. Of the summer aspect *Prosopis farcata*, *Crotophora tinctoria*, *Malvella sherardiana*, *Lavatera trimestris*, *Heliotropium europaeum* and *H. villosum* are most characteristic.

These are only some of the most noxious weeds of the Palestine agricultural plains (Zohary, 1941). Among the other associations of this union we wish to mention *Prosopis farcata*-*Carthamus glaucus* association (Beisan Valley), *Prosopis farcata*-*Alhagi maurorum* (less deep soils).

Irrigated fields harbour the *Prosopis farcata*-*Panicum colonum* association in which *Prosopis* is again the dominating plant, but it is associated by a rather hydrophilous flora such as *Panicum colonum*, *P. sanguineum*, *Setaria verticillata*, *Portulaca oleracea*, *Amaranthus graecizans*, *A. retroflexus*, *Albersia blitum*, etc.

(2) *Ononideto-Carthamion*. This group is confined mainly to segetal habitats of the mountain region. It comprises the *Carthamus tenuis*-*Ononis leiosperma* association which similarly exhibits spring and summer aspects. In winter the greatest number of the associates are flowering, for instance, *Leontice leontepetalum*, *Bongardia chrysogonum*, *Astoma seselifolium*, *Calepina irregularis*, *Neslia paniculata*, *Sinapis arvensis*, *Bromus macrostachys*, *Phalaris brachystachys*, *P. nodosa*, *Asperula arvensis* and *Aristolochia maurorum*. In summer it is *Carthamus* and *Ononis*, especially the former, which cover the mountain fields, associated with *Convolvulus arvensis*, *Chrozophora tinctoria*, *Heliotropium villosum* and *H. europaeum*.

Another association is *Centaurea iberica*-*Cirsium acarne*, known from Upper Galilee and Transjordan. We have not yet studied this association in detail.

(3) *Achilleion santolinae* (Zohary & Feinbrun, 1942). This is confined to the loess soils (Negeb, Transjordan). The associations belonging to this group differ according to the texture and lime content of soil. Most abundant are the *Achillea santolina*-*Hyoscyamus reticulatus* association and the *Achillea santolina*-*Ixiolirion montanum* association. The former includes, apart from the two leading species, *Trigonella arabica*, *Salvia lanigera*, *Muscari longipes*, *Coronilla repanda*, *Silene colorata*, *Glaucium corniculatum*, *Plantago albicans*, *Astragalus alexandrinus* and the most important *Thesium humile*, one of the most noxious weeds of this area.

## VIII. SUMMARY

1. A review of the vegetation units of all Palestine as related to ecological factors has been given.

2. Stress was laid on the natural classification of the vegetational groups which, though some of them are only tentatively denominated, may facilitate the understanding of the entire vegetation cover of the country, and serve as a basis for future ecological studies in this region.

3. In mapping and analysing vegetation the author applied a somewhat special method—the triple method—according to which the climax associations, one of the permanent stages of the sere, and the segetal association of each area were taken as a

*taurea procurrens* association; C, *Ormenidetum* mixtae and allies.

11. A, *Quercus ithaburensis-Pistacia atlantica* association; B, ?; C, association of *Prosopidion farcatae* and *Zizyphion spina christi*.

12. A', as in 1?; B, semisteppe Batha association (e.g. *Convolvulus dorycnium-Carlina corymbosa* association, *Psoralea bituminosa-Echinops blanceana* association), *Salvia graveolens-Ballota undulata* association; C, *Centaurea iberica-Cirsium acarne* association or *Carthametum glauci*.

13. A', as in 11; B, as in 12; C, ?.

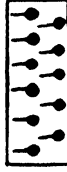
14. A', ? or rarely as in 1 or 7; B, semisteppe facies of *Poterietum spinosi*; C, as in 1.

15. A', semisteppe forest of *Crataegus azarolus* or *Prunus amygdalus* or *Pistacia atlantica*; B, semisteppe facies of *Poterietum spinosi*, *Calycotometum villosae* and association of *Varthemion* and semisteppe Batha (mainly of *Salvia-Ballota* association, *Ononidetum natricis*, etc.).



(sandy loess).

28. *Salsolietum villosae* (alluvium and Lissan marl).



29. Non-halophytic desert association of *Anabasion articulatae* (Hammada), *Suaedion asphalticae* (gypseous desert soil), *Zygophyllion dumosi* (rocky deserts).



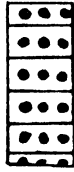
30. Halophytic association of *Junceto-Phragmition*, *Tamaricion tetragynae*, *Atripliceto-Suaedion*.



31. Hydrophytic association of *Potamion*, *Phragmition* (including *Cyperetum papyri* of Huleh swamps), *Populion euphraticae* (Jordan Valley); *Rubion sancti*, *Nerion oleandri*, etc.



32. Vegetation of Sudano-Deccanian enclaves (oases), mainly *Zizyphus spina christi-Balanites aegyptiaca* association.



33. Relics of *Acacietum albidae*.



34. *Cynodon dactylon-Centaurea iberica* association.







combined expression of each vegetational area (within the Mediterranean and partly also within the Irano-Turanian territories).

The writer has used in this review, among others, unpublished papers of Feinbrun & Zohary, 'Studies on the vegetation of Transjordan'; of Zohary & Feinbrun, 'Outline of the vegetation of the Negeb (Southern Palestine)'; and of Zohary & Orshansky, 'Geobotanical studies in the salt lands of the Dead Sea Region'.

The writer wishes to express his thanks to Mr Grizi for his field and laboratory aid in connexion with this paper as well as to his son, Daniel Zohary, who helped him greatly in field work.

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# OBSERVATIONS ON THE ECOLOGY OF THE BUDONGO RAIN FOREST, UGANDA

By W. J. EGGELING

*Conservator of Forests, Uganda Protectorate*

(With Plates 1-3, two Maps, and nine Figures in the Text)

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## I. INTRODUCTION

Elsewhere (Eggeling, 1940*a*) I have given an account of Budongo from the aspect of timber production and replacement, with brief notes on composition. In the present paper the vegetation of the forest is described in greater detail, but I wish to emphasize that my observations have been general rather than particular. Budongo makes an excellent subject for the study of the ecology of rain forest. It is one of the few rain forests in Africa which is increasing in size, and therefore one of the few in which can be observed the development of climax rain forest through all the stages following the initial colonization of grassland. The object of this paper is to describe these various stages in so far as the natural succession is concerned. Secondary types, such as regrowth after exploitation, are not included. Most emphasis is laid on woody growth, since it is this, chiefly, which has been studied. There is much scope for further work, for example, in the study of soils

and soil preferences, in detailed investigation of the ecology of the undershrubs, herbs, climbers and epiphytes, in determining the shade resistance and shade tolerance of the various species, etc.

To facilitate comparison with descriptions of rain forests elsewhere in the tropics, the subject-matter is presented in a form generally similar to that adopted by Richards (1939) in his account of the rain forest of Southern Nigeria and in his earlier studies of the forests of British Guiana and Sarawak (Davis & Richards, 1933 and 1934; Richards, 1936).

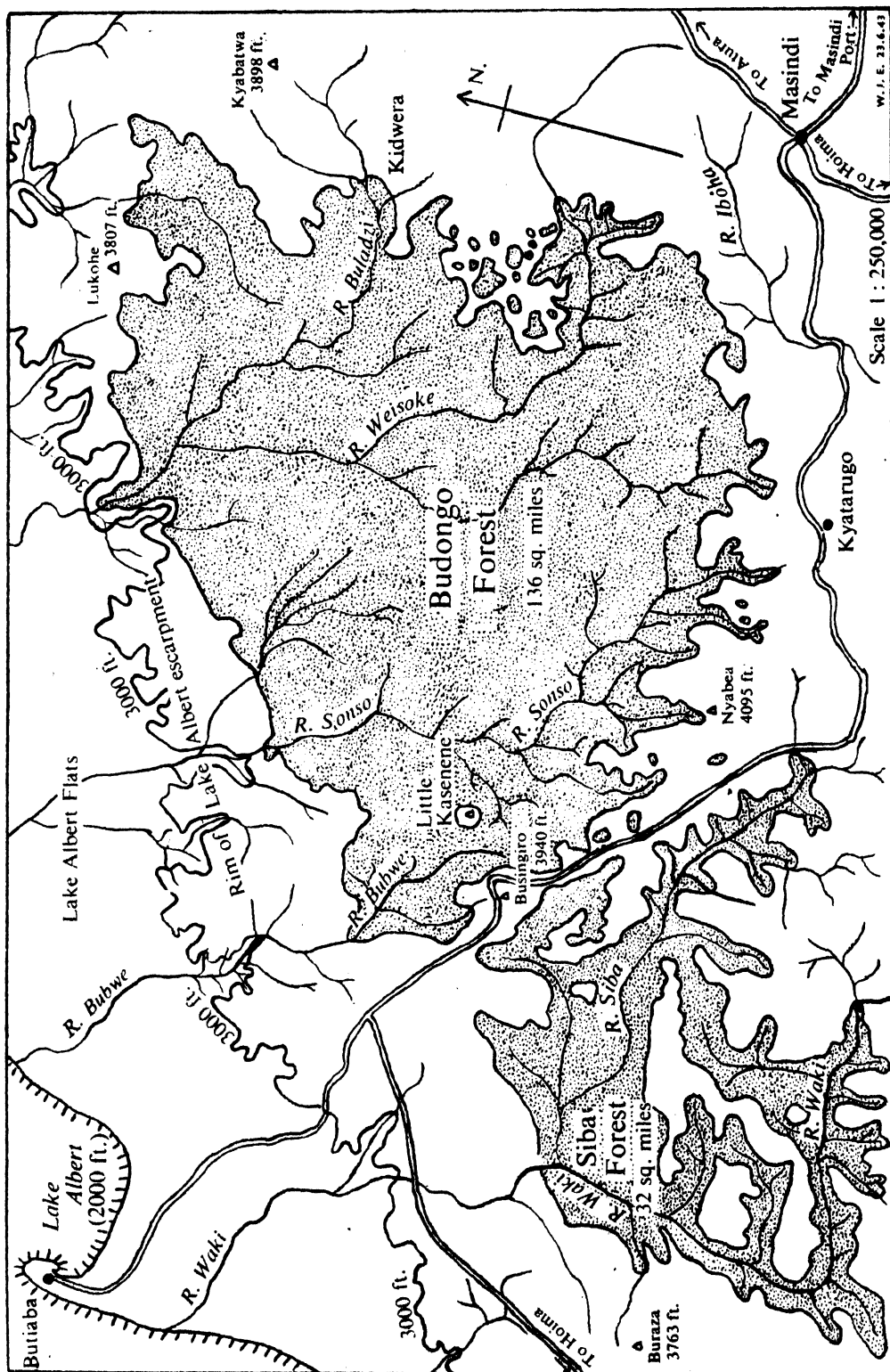
## II. HABITAT

### (1) *Situation and topography*

The Civil District and Native Kingdom of Bunyoro, which contains the Budongo forest, forms part of the Western Province of the Uganda Protectorate. It is bounded on the west by Lake Albert, on the north and east by the Victoria Nile, and on the south by the Kafu and Nkusi rivers (which rise in the same swamp but drain in opposite directions to the Victoria Nile and to Lake Albert respectively). The Masindi Port to Butiaba road which crosses the District from east to west divides Bunyoro into two almost equal parts and separates the Siba portion of Budongo from Budongo proper (Map 1). About 47 km. (30 miles) to the west of Masindi Port (1021 m. = 3350 ft.) lies Masindi (1146 m. = 3760 ft.), the headquarters of the Province. Stretching between Masindi and Hoima (1158 m. = 3800 ft.), 56 km. (35 miles) to the south-west, a ridge of hills forms a backbone to the District. South and east of these hills the streams drain to the Kafu and thence to the Nile. West of the range they drain direct to Lake Albert (619 m. = 2035 ft.). The Budongo forest lies towards the north end of the lake, on the gentle upper slopes of the watershed, with its western edge only 3–6 km. (2–4 miles) from the top of the escarpment. From the rim of the scarp the ground falls steeply for over 300 m. (1000 ft.) to the flatlands bordering Lake Albert. The forest is situated between latitudes  $1^{\circ} 35'$  and  $1^{\circ} 55' N.$ , and between longitudes  $31^{\circ} 18'$  and  $31^{\circ} 42' E.$  It has an average altitude of about 1100 m. (3600 ft.).

As shown on Map 1, Budongo proper is a solid mass of forest 35,200 ha. (136 sq. miles) in area. The Siba forest (8300 ha. = 32 sq. miles) consists of a more or less compact central portion some 3100 ha. (12 sq. miles) in extent, together with about 5200 ha. (20 sq. miles) of narrow strips of gallery forest on the banks of the Siba and Waki rivers and their tributaries.

In the Budongo portion of the forest, the ground is undulating. The valley bottoms are generally soft, and many of the so-called streams are mere trickles through rattan (*Calamus*) swamp, with no apparent flow in dry weather. The general direction of the numerous valleys is from south-east to north-west, but not infrequently the streams turn for short distances at right angles along small fault lines or joint planes. As they approach the western margin of the forest the majority of the watercourses join to form two rivers which run in slightly deeper valleys, the Sonso and Weisoke. In the wet season these rivers may be up to 120 cm. (4 ft.) deep. In the dry season the Sonso often dries completely. The whole area is well weathered, slopes are with few exceptions gradual, and the intervening ridges are rounded. North of Budongo, in grassland, are two prominent isolated hills, Lukohe (1160 m. = 3810 ft.) and Igissi (1270 m. = 4170 ft.). There are similar hills at intervals along the western and southern edges of the forest, including Nyabea (1250 m. = 4090 ft.) and Busingiro (1200 m. = 3940 ft.) on the Masindi-Butiaba road.



Map 1. Budongo and Siba forests, Bunyoro.

These sentinel hills are features of the landscape and afford splendid views. About 2.5 km. (1½ miles) north-east of Busingiro lies the pimple-like Little Kasenene (1175 m. = 3850 ft.), the only grass-covered hill within the forest (Pl. 1, phot. 1).

## (2) *Geology and soil*

The Albert rift, as it now exists, owes its formation to earth movements which began in late Pliocene times and continued throughout the Pleistocene era. These movements had an important bearing on the configuration and soils of Bunyoro. Rise in level of the sides of the rift, accompanied perhaps by depression of the bottom, first led to river reversal along the rift crest. Later, towards the end of the Pleistocene, it is probable that further movements of a 'rapid' kind gave the pronounced escarpment with its hanging topography.

It is accepted generally that advanced lateritization coincided in Uganda with peneplanation. The fact that peneplanation occurred in Bunyoro is obvious from the flat-topped hills in the centre of the District, but although a lateritic blanket presumably once cloaked the whole of the present forested area, when at its former level, very little trace of that blanket remains to-day. The hills which surround the forests indicate the past level, and it is clear that there has been much erosion. It is possible that, following the rift uplift, widespread erosion removed the greater part of the laterite and led to the formation of fresh and fertile soils, some of which were quickly colonized by forest.\*

Crystalline rocks of the Ancient Basement Complex, intruded by granites, underlie Budongo. From these rocks the soils derive. The Basement Complex, 'whose age is probably one thousand five hundred million years, . . . is an assemblage of schistose and gneissose rocks which are highly metamorphosed sandstones, shales, limestones, and eruptives originally brought into being under physical conditions differing in no way fundamentally from those of to-day' (Thomas & Scott, 1935).

Over a small section of the southern part of the Siba forest the Basement Complex rocks are masked by overlying sediments of the Bunyoro Series. This Precambrian glacial series is a less altered and almost certainly younger development of the Karagwe-Ankolean Series. It 'consists of mudstones, shales, phyllites (altered shales, originally clays), sandstones, quartzites (altered sandstones, originally sand), and conglomerates, and contains some more or less calcareous zones. An important feature of the series is a well-marked glacial horizon represented by glacio-fluviatile deposits, outwashed gravels and tillite—a solidified, and somewhat altered, boulder clay indicative of low-level glaciation almost on the Equator. The Bunyoro Series has suffered less from distortion than the Karagwe-Ankolean beds, but is considerably cut up in a quadrangular fashion by large-scale faulting' (Thomas & Scott, 1935). Except to the south of the Siba forest, where

\* The suggestion that the situation and extent of the Budongo and Siba forests may have been determined by past erosion was first put forward by Harris (1935). His views were queried by Bourne, of the Imperial Forestry Institute, in a minute dated 18 October 1933. Bourne thinks it more probable that the forests are relics of a previous and moister climatic era during which a much larger forest belt was slowly reduced in extent, the denuded soils becoming lateritized on exposure to heat under conditions of high rainfall. It is not obvious why a moister era, as envisaged by Bourne, should have seen a reduction in the size of forests which under present-day (dry) conditions are steadily expanding. Shrinkage during a dry era, with lateritization during a subsequent wet period, would be understandable, but had this happened more traces of lateritization would be expected than actually exist.

some of the surrounding hills show sheer granite faces, it is only in the beds of streams that much parent rock is visible.

There are two main types of soil, a tropical red earth and a murram. The first, which is by far the more abundant, is red in profile and varies from a heavy loam or sandy clay to a very sandy loam characteristic of many of the valley bottoms. Immediately below the 5–10 cm. (2–4 in.) of the humus-rich surface horizon this soil is usually less clayey and more sandy than at greater depth.

In the second chief type of soil (the murram), the hydration and redeposition of iron and aluminium probably occurred *in situ*. This is inferred from the fact that such soil is generally found on relatively low and rounded ridges or on gentle slopes, and is always underlain by quartzose rocks. The nature of the material supports the suggestion that its formation predates the final rift movement. Within the forests, soil of this type is very local and covers relatively small areas. It varies in character from a red loam containing small ironstone concretions, capable of supporting forest, to tiny ridge-top pavements of solid cellular ironstone, which can hardly be classed as soil and are completely barren.

Table 1. *Available plant nutrients and soil reaction, Budongo soils.\**

	Available nutrients				Reaction (pH)
	Nitrates	Phosphates	Potassium	Calcium	
A. Ironwood Forest in S.P. 2 (Pit 1):					
A1 horizon	—	2	1	3	6.6
B1 horizon	—	1	0	2	6.2
B2 horizon	—	0	0	1	5.6
C horizon	—	1	1	1.5	5.6
B. Mixed Forest in S.P. 3 (Pit 2):					
A1 horizon	—	1	1.5	2	6.2
B1 horizon	—	2	0	2	5.5
B2 horizon	—	0	0	1	4.8
C1 horizon	—	0	0	1	4.6
C2 horizon	—	1	1	1	4.6
C. Mixed Forest (Pit 3):					
A1 horizon	—	2.5	1	3	6.8
B1 horizon	—	2	1	2	6.6
B2 horizon	—	1	1	1.5	6.4
C horizon	—	0	0	0	5.2
D. Mixed Forest: A1 horizon	1	0.5	2	1	6.0
E. <i>Maesopsis</i> Forest in S.P. 7 (Pit 4): A1 horizon	0	0	2	2	6.5
F. <i>Acanthus</i> belt separating <i>Maesopsis</i> Forest and <i>Hyparrhenia</i> Grassland: A1 horizon	1	0	1	1	6.0
G. <i>Hyparrhenia</i> —Small Tree ( <i>Combretum</i> ) Grass- land, base of Busingiro Hill (Pit 5):					
A1 horizon	—	1.5	1.5	3	7.1
B1 horizon	—	0	0	1.5	6.6
C horizon	—	0	1	1.5	6.6
H. <i>Hyparrhenia</i> —Large Tree ( <i>Terminalia</i> ) Grass- land, Biiso: A1 horizon	1	0.5	0	1	5.5
I. <i>Hyparrhenia</i> —Large and Small Tree Grassland, Busingiro Hill: A1 horizon	0	1	2	1	6.0
J. Poor <i>Hyparrhenia</i> Grassland on murram soil, Nyakafunjo: A1 horizon	0.5	0	0.5	0.5	5.5

\* Available plant nutrients (nitrates for a few samples only) estimated by the method described by Spurway (1938), on a scale of 0–4; reaction tested by B.D.H. Universal Indicator. S.P. indicates sample plot number throughout the paper.

There is little doubt that the forests of Central Africa were once vastly more extensive than they are to-day, but because laterite is unlikely to have formed under a forest canopy it is probable also that the wooded area of Budongo has been smaller than it is now. This supposition is borne out, as will be shown, by the vegetation.

Wayland (1933), in a summary of the major physiographical events in Uganda from the end of Pleistocene times up to the present, has envisaged considerable fluctuations in temperature and moisture during Pleistocene and subsequent times. It would seem a fair assumption that the forest likewise fluctuated, not only in extent but also in the nature and abundance of the constituent species, receding in droughts and spreading in times of high humidity. At the moment the balance is weighted, albeit ever so slightly, in the forest's favour.

*Soil profiles.* Descriptions of soil profiles in the main types of forest are given below. Analyses are listed in Table 1.

*Pit 1.* Ironwood Forest, Siba (near S.P. 8)

Forested lower slopes of grass-topped hill. Very gentle north-west slope. Slight north-west exposure. *Cynometra* the dominant large tree; *Lasiodiscus* understory. Woody herbs and abundant *Lasiodiscus* regeneration around pit. Shade at ground level complete and dense.

*Horizons:* A0. 0–1.25 cm. (0–0.5 in.). Black. Leaf litter.

- A1. 1.25–6 cm. (0.5–2.5 in.). Dark brown, merging with the red-brown of horizon B1. Loam. Many rootlets; a few roots up to 1.25 cm. (0.5 in.) diam.
- B1. 6–30 cm. (2.5–12 in.). Red-brown. Friable loam. Many rootlets; one root 5 cm. (2 in.) diam., two roots 10 cm. (4 in.) diam. Termites.
- B2. 30–135 cm. (12–54 in.). Red. Clay; slightly angular near base of horizon. Some fibre; a few roots 2.5 cm. (1 in.) diam.; one root 7.5 cm. (3 in.) diam. Several termite shafts about 25 cm. (10 in.) high.
- C. 135–244 cm. (54–96 in.). Brick-red. Angular clay. Horizon crowned with layer of gravel 15 cm. (6 in.) thick; quartz veins throughout. Fibre rare; several rotted roots. One yellow streak due to decomposing rock.

*Pit 2.* Ecotone between Mixed Forest and Ironwood Forest, Budongo (near S.P. 7).

Very gentle westerly slope. West-north-west exposure. Trees near pit include *Khaya*, *Cynometra*, *Celtis* spp., *Alstonia*, *Lasiodiscus*, *Funtumia elastica* and *F. latifolia*. Undershubs 3–4 m. (10–12 ft.) high, and scattered herbs, border the pit. Nearest trees 1.8, 2.7 and 3.6 m. (6, 9 and 12 ft.) distant. Shade complete.

*Horizons:* A0 and A1. 0–5 cm. (0–2 in.). Brown. Loam. Many rootlets.

- B1. 5–40 cm. (2–16 in.). Brownish, becoming paler. Angular clay. Many rootlets and roots, up to 5 cm. (2 in.) diam.
- B2. 40–135 cm. (16–54 in.). Red. Angular clay. Roots fairly abundant, ranging from fibre up to roots 5 cm. (2 in.) diam. Red streaks rare. One termite shaft.
- C1. 135–160 cm. (54–64 in.). Brick red. Extremely hard gravelly angular clay. Continuous layer of gritty rubble at base of horizon. Rootlets rare. Red concretionary streaks common; purple spots occasional. Fair number of yellow weathered stones.
- C2. 160–205 cm. (64–82 in.). Clay in angular fragments. Local veins of weathered schist. Rootlets occasional. Scarlet concretionary streaks; yellow decomposed pebbles.

*Pit 3.* Mixed Forest, Budongo.

Gently undulating with small steep side valleys. Pit near crest of an undulation, just above a valley. Nearby trees include *Alstonia*, *Cynometra*, *Entandrophragma cylindricum*, *E. utile*, *Celtis* spp. and *Lasiodiscus*. Aspect north. Exposure sheltered, slightly south and north-east. Slope gentle, becoming steeper about 90 m. (295 ft.) from pit. Shade complete.

*Horizons:* A1. 0–6.5 cm. (0–2.5 in.). Brownish black, merging with the brown of the B1 horizon. Silty and greasy. Much fibre; many rootlets and roots, up to 6.5 cm. (2.5 in.) diam. Structure cubical. Limit ill-defined. Many large earthworms.

- B1. 6.5–25 cm. (2.5–10 in.). Brown. Silt with fairly high clay content, gritty to the touch. A little fibre in humus downwash; roots up to 1.25 cm. (0.5 in.) diam. Some fine gravel. Structure cubical-rounded. Humus carried down root channels showing as grey-brown bands. Lower limit clearly defined.



- B2. 25–85 cm. (10–34 in.). Red-brown. Gritty clay. Many rootlets and roots, up to 2.5 cm. (1 in.) diam. Much gravel and many pebbles up to 1.25 cm. (0.5 in.) diam. Vertical red concretional streaks. Structure of large vertical plates fracturing into rough cubes. Very compact. Humus carried down root channels showing as grey-brown bands.
- C. 85–180 cm. (34–72 in.). Red. Clay. Some rootlets, 1 root 1.5 cm. (0.5 in.) diam. Some gravel. Yellow concretional blotches. Structure of vertical plates fracturing into rough cubes. Very compact.

*Pit 4. Colonizing (Maesopsis) Forest, Budongo (in S.P. 3).*

Level top of low ridge. *Maesopsis* the dominant tree near pit. Other species include *Caloncoba*, *Phyllanthus discoideus*, and *Funtumia latifolia*. Shade medium-dense.

- Horizons:* A1. 0–18 cm. (0–7 in.). Dark brown, merging with the red-brown of the B1 horizon. Clay loam with high clay content. No gravel. Topmost 2.5 cm. (1 in.) full of fibre; rootlets common; roots up to 2.5 cm. (1 in.) diam. Water percolating through one hollow root.
- B1. 18–30 cm. (7–12 in.). Red-brown. Clay, containing particles of gravel and of decomposing roots. Rootlets and roots, up to 2.5 cm. (1 in.) diam.
- B2. 30–48 cm. (12–19 in.). Red. Clay (drier than that of B1 horizon), containing gravel in the form of angular lumps or rounded (weathered) quartz crystals. Occasional fibre and rootlets.
- C. 48 cm. (19 in.) down. Reddish yellow with yellow streaks of decomposed granitic gneiss. Rootlets and fibre occasional.

*Pit 5. Hyparrhenia-Small Tree (Combretum) Grassland, Budongo.*

Uniform gentle slope with eastern aspect at base of Busingiro hill near forest edge. Drainage free. *Hyparrhenia cymbaria* the dominant grass. Scattered small trees (chiefly *Combretum binderanum*). Pit shaded by grass only.

- Horizons:* A1. 0–10 cm. (0–4 in.). Black drying to grey, merging with the dark brown of the B1 horizon. Litter practically absent. Clay, soapy when wet. Much fibre; rootlets and roots, up to 1.25 cm. (0.5 in.) diam. Much mycorrhiza.
- B1. 10–40 cm. (4–16 in.). Dark brown with grey-brown streaks, merging with the tawny brown of the B2 horizon. Clay, containing ironstone concretions 2.5–4 cm. (1–1.5 in.) diam. Rootlets and roots up to 1.25 cm. (0.5 in.) diam. Termite shafts allow humus penetration.
- B2. 40–160 cm. (16–64 in.). Tawny brown. Silty clay. Scattered fibre and rootlets. Earthworms low in horizon. Termite shafts.
- C. 160 cm. (64 in.) down. Tawny with bright red streaks. Clay.

### (3) *Climate\**

In 1937, at the suggestion of the Imperial Forestry Institute, the Uganda Forest Department began an investigation of the microclimates of the Budongo forest. Four meteorological stations were opened inside the forest, with a fifth station (the control) just outside. The data obtained up to the end of 1942 are being analysed by the Director of the British East African Meteorological Service, and only a few results (which may require slight modification in the final report) are yet available. Meanwhile, therefore, practically the only figures which can be considered in detail come from stations close to but *outside* the forest, so that only the *general* climate, and not the internal climate, can be described.

\* With the exception of the data for Busingiro, Masindi Port and Kyatarugo, all the figures quoted are from Walter (1940).

(i) *Rainfall*

A series of recording stations, from which rainfall figures are available for periods of from 10 to 40 years, stretches across Bunyoro from Masindi Port to Butiaba. The average annual precipitation at Masindi Port is only 1041 mm. (41.0 in.), but Butiaba on the rift floor has even less with an average of 818 mm. (32.2 in.). This is scarcely half the probable rainfall over the Budongo forest, not 16 km. (10 miles) distant. Above the escarpment, the rainfalls at the three recording stations nearest the forest (Masindi, Kyatarugo and the Budongo (Mile 55) Camp at Busingiro) have annual averages of 1296 mm. (51.0 in.), 1410 mm. (55.5 in.) and 1495 mm. (58.8 in.) respectively, the gauges being 5.5 km., 3.5 km. and 180 m. ( $3\frac{1}{2}$  miles,  $2\frac{1}{2}$  miles, and 200 yd.) from the edge of the forest. In Bunyoro, rain is extremely local, so that it is rare to find any two stations recording even approximately the same fall on any one day. At most stations there is a much closer correspondence from year to year in the number of rainy days (days on which 0.25 mm. (0.01 in.) or more of rain are recorded) than in actual precipitation, the latter frequently varying greatly from one year to the next. Thus at Kyatarugo Estate, the 21 years 1916-32 and

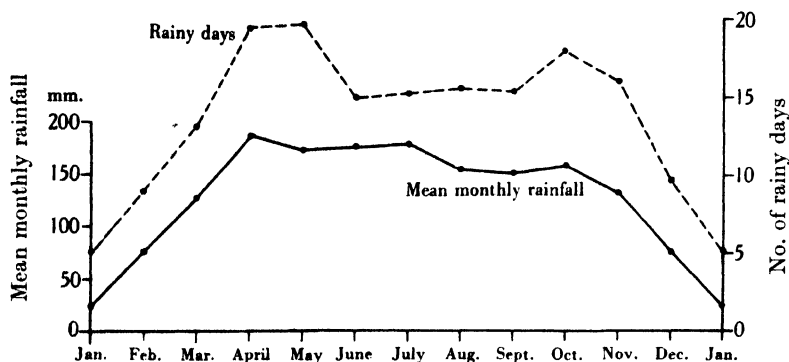


Fig. 1. Rainfall at Budongo (Mile 55) Camp, Busingiro, Bunyoro, for the period August 1933-July 1943.

1939-42, there were only 4 years with less than 130 rainy days,\* and only 4 years† with more than 146. In 13 of these 21 years, therefore, there were between 130 and 146 rainy days in the year, but in the same 13 years the rainfall varied from 1191 mm. (46.9 in.) in 1925 to 1818 mm. (71.6 in.) in 1928. At Busingiro, nearer the forest, the number of rainy days is higher than at Kyatarugo (Table 5).

The rainfall of Bunyoro is of the double-peak type (Fig. 1). It is in most parts well distributed, especially in the centre of the District. There is a pronounced dry season from mid-December through January to mid-February. At Busingiro these 3 months all show a mean rainfall of less than 80 mm. (3.1 in.), the driest (January) averaging only 23 mm. (0.9 in.); April and May, and August to October are the wettest seasons (Table 2). At Busingiro the mean rainfall during the early rains is almost the same as that during the late rains, but owing to variation in distribution from year to year the main fall may come either in the first half of the year or in the second. Rain is commoner in the afternoons and evenings than at other times.

Because of its situation, Busingiro probably gives a better indication of the rainfall of Budongo than either Masindi or Kyatarugo. Even so, the mean annual precipitation of 1495 mm. (58.8 in.) at Busingiro is without doubt well below that over the forest. From

\* 116 in 1927; 125 in 1930; 126 in 1942; 127 in 1926.

† 163 in 1917 and 1919; 158 in 1916; 157 in 1929.

the vantage point of Budongo Forest Station, on the slopes of Busingiro hill, it is noticeable that many of the storms which break over the forest never reach its edge. Moreover, because the great majority of the storms come from the north-east, rain seldom falls at Busingiro without falling on the forest also. Frequently, when I have been on safari in Budongo, rain has fallen on my camp when none has been recorded outside the forest. Taking a year at random, I was camped in Budongo in 1933 from 15 to 27 September and again from 7 to 13 December. During the September safari, rain fell in the forest on 11 of the 13 days; during that of December on 6 out of the 7. In the same periods rain was recorded at Busingiro on only 7 and 3 days respectively. Such experiences are typical.

The average annual rainfall over Budongo probably lies between 1780 and 1900 mm. (70–75 in.), but actual measurements are necessary. Unfortunately, rainfall measurement was not included in the study of microclimates to which mention has been made above, but a rain gauge has lately (1944) been set up in the middle of the forest, so that figures will be available in the future.\*

Table 2. *Monthly rainfall (mm.) at Budongo (Mile 55) Camp, Busingiro, Bunyoro, for the period August 1933–July 1943*

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1933	—	—	—	—	—	—	—	181.9	246.9	141.5	137.4	38.9	(746.6)
1934	1.5	5.6	112.5	154.9	106.2	50.3	67.8	115.3	73.4	188.0	145.5	62.0	1083.0
1935	6.1	36.1	122.4	170.2	258.1	271.8	47.2	104.9	148.6	258.1	120.7	184.1	1728.3
1936	40.4	150.6	199.1	147.3	194.1	253.2	131.3	87.9	141.9	172.0	103.1	118.4	1739.3
1937	8.6	106.2	131.1	218.4	125.0	200.2	127.3	41.7	169.4	240.0	198.4	36.6	1602.9
1938	2.5	33.8	60.2	243.6	191.8	141.2	171.7	153.4	115.6	225.0	75.2	35.8	1449.8
1939	30.2	88.4	91.6	167.9	120.9	133.6	118.9	186.4	232.2	77.5	151.9	29.7	1429.2
1940	50.0	153.2	133.1	214.9	134.9	67.1	120.9	196.3	115.6	155.7	112.0	30.5	1484.2
1941	30.7	56.9	89.9	176.0	176.0	29.7	55.6	218.9	174.2	72.9	213.9	116.3	1411.0
1942	64.8	90.4	262.6	155.2	220.2	80.5	33.8	260.4	108.0	65.5	58.7	76.2	1476.3
1943	0.0	53.6	89.4	233.9	198.6	110.2	109.5	—	—	—	—	—	(795.2)
Average, 10 years (nearest mm.)	23	77	129	188	173	134	98	155	153	160	132	73	1495

There is a local belief that the rainfall of Bunyoro is increasing. It derives from a superficial examination of records such as those from Kyatarugo estate, where towards the end of the period 1914–32 there was a marked increase in average precipitation. The mean annual rainfall for the first 14 years of the sequence was only 1303 mm. (51.3 in.), but for the final 5 years was 1778 mm. (70 in.). To determine the value of such figures I have prepared graphs (Fig. 2) of rainfall trend at four localities in Bunyoro, utilizing rainfall data from seven stations. The graphs show conclusively that at no locality has there been a significant increase in rainfall since recording began, increases over short periods being counterbalanced by decreases shortly afterwards.

## (ii) *Temperature*

Considering its situation and its elevation, Bunyoro has very equable temperatures (Table 3). This may, of course, be attributable to its forests.

At Masindi, the mean maximum temperature is 29.8° C., the mean minimum temperature 16.7° C., and the mean diurnal variation 13.1° C. At Busingiro, the corresponding figures are 28.3, 14.1 and 14.2° C. The variation in the monthly means of the diurnal range is very small (only about 5° at Masindi and about 4° at Busingiro). The smallest mean diurnal range is experienced in July, August and September (10–11°), and the

\* 1945 figures were: middle of forest, 1842 mm. (69.53 in.); Busingiro, 1414 mm. (55.68 in.).

greatest in the dry-season months of January and February ( $13-16^{\circ}$ ), when temperatures generally are higher. July is the coolest month of the year and February (sometimes January) the hottest. Figures for a typical month (June) of a typical year (1942) at Busingiro are:

	Month (June 1942) ( $^{\circ}$ C.)	Year (1942) ( $^{\circ}$ C.)
Highest daily maximum	31.7	35.0
Lowest daily maximum	24.9	21.1
Highest daily minimum	16.7	18.0
Lowest daily minimum	11.0	10.0

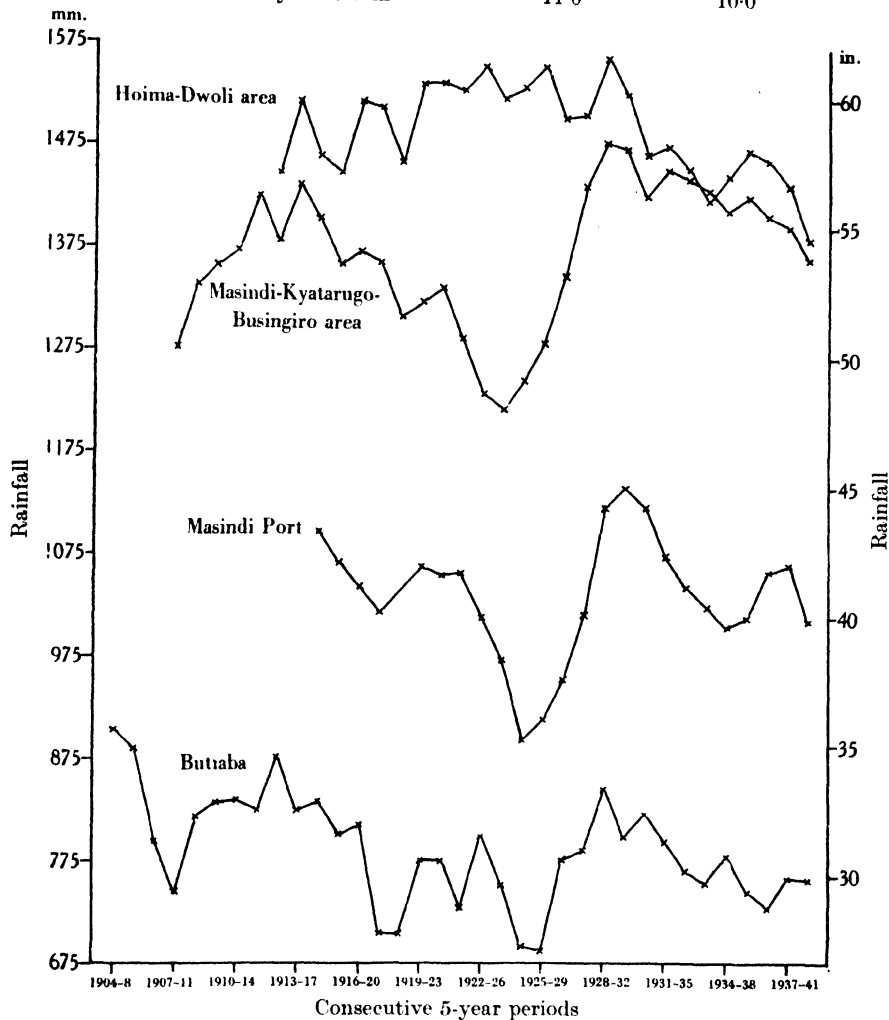


Fig. 2. Rainfall trend, Bunyoro, for four localities. (Method of consecutive periodic means.)

The variation between monthly absolute temperatures is surprisingly constant. In no month of the year does the absolute maximum temperature exceed the absolute minimum by more than  $25^{\circ}$  or by less than  $19^{\circ}$ .

The difference between screen temperatures outside and inside the forest is not great, as can be seen from the following figures (years 1939-41 inclusive). Soil temperature is shown also:

Station	Screen temp. ( $^{\circ}$ C.)				Soil temp. ( $^{\circ}$ C.)
	Mean max.	Mean min.	Range	Mean	
No. 1. Outside the forest (control station)	28.2	14.6	13.6	21.4	24.3
No. 2. Inside the forest (near S.P. 8)	25.7	14.5	11.2	20.1	19.9

Table 3. *Shade temperatures at Butiaba, Masindi and Hoima, Bunyoro (° C.)*

Month	(1) Mean temperature of the air			(2) Mean maximum temperature			(3) Mean minimum temperature		
	Butiaba	Masindi	Hoima	Butiaba	Masindi	Hoima	Butiaba	Masindi	Hoima
Jan.	25.4	22.6	23.8	29.8	31.9	31.4	21.9	15.8	17.1
Feb.	26.0	22.6	24.5	29.9	31.7	31.8	22.8	15.7	18.1
Mar.	25.4	21.8	23.5	29.0	29.9	30.1	22.6	16.6	17.9
Apr.	25.4	22.2	23.1	29.2	30.0	29.1	22.5	17.1	17.9
May	25.4	22.5	22.2	29.0	30.5	27.8	22.4	18.1	17.5
June	25.2	21.9	22.1	29.0	30.0	27.9	22.2	17.0	17.1
July	24.4	20.7	21.1	27.9	28.3	26.3	21.9	16.6	16.8
Aug.	24.5	20.8	21.4	28.1	27.6	26.9	22.0	16.6	16.7
Sept.	24.7	21.2	21.6	28.2	28.7	27.5	22.0	16.9	16.7
Oct.	24.9	21.5	21.8	28.6	29.5	27.8	22.2	17.0	16.8
Nov.	25.0	22.0	22.4	28.7	29.8	28.8	22.3	17.0	16.9
Dec.	24.8	21.6	22.2	28.9	29.6	29.0	21.8	16.4	16.4
Year	25.1	21.8	22.4	28.8	29.8	28.7	22.2	16.7	17.2

Month	(4) Mean daily range of temperature			(5) Absolute maximum temperature			(6) Absolute minimum temperature		
	Butiaba	Masindi	Hoima	Butiaba	Masindi	Hoima	Butiaba	Masindi	Hoima
Jan.	7.9	16.1	14.3	33.4	36.7	34.4	18.3	11.9	11.1
Feb.	7.1	16.0	13.7	33.9	36.0	36.1	19.4	15.9	15.0
Mar.	6.4	13.3	12.2	32.2	34.6	33.9	19.7	9.4	15.0
Apr.	6.7	12.9	11.2	31.7	33.9	32.8	19.0	11.1	14.4
May	6.6	12.4	10.3	31.1	34.4	32.8	19.4	14.3	14.4
June	6.8	13.0	10.8	32.0	34.4	30.6	19.4	12.4	13.9
July	6.0	11.7	9.5	30.9	34.6	30.0	16.9	11.8	12.2
Aug.	6.1	11.0	10.2	30.7	34.4	30.0	18.9	11.9	11.7
Sept.	6.2	11.9	10.8	31.8	35.6	31.1	18.0	13.6	12.8
Oct.	6.4	12.5	11.0	31.7	36.7	31.1	18.9	14.7	15.0
Nov.	6.4	12.8	11.9	32.3	36.7	32.2	18.6	14.2	14.4
Dec.	7.1	13.2	12.6	35.1	35.6	33.3	17.6	13.3	13.3
Year	6.6	13.1	11.5	35.1	36.7	36.1	17.6	9.4	11.1

Altitudes are: Butiaba, 619 m. (2030 ft.); Masindi, 1146 m. (3760 ft.); Hoima, 1158 m. (3800 ft.).

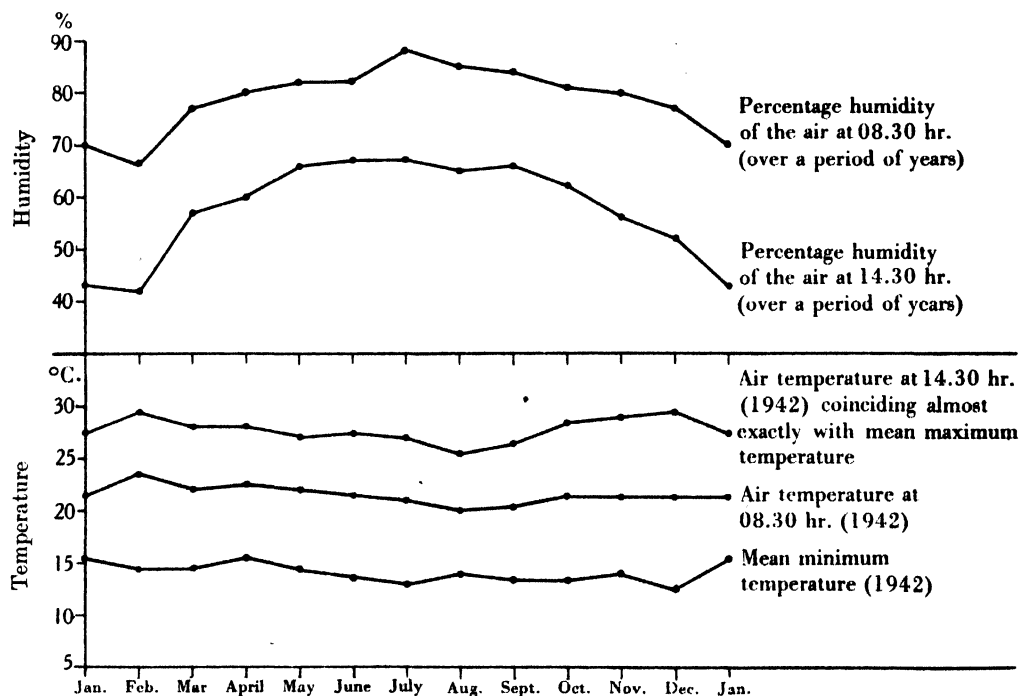


Fig. 3. Mean maximum, minimum and air temperatures at Budongo (Mile 55) Camp, Busingiro, Bunyoro; and mean percentage humidity of the air at Masindi, Bunyoro.

(iii) *Wind, humidity, vapour pressure, etc.*

*Wind.* During periods of fine weather there is a fairly constant light breeze both by day and by night in the vicinity of Budongo. At Busingiro the rain-bearing winds nearly all come from the north-east (i.e. from over the forest). Rain from the north-west is rare. In the Siba area, the majority of the rain comes from the south and south-west.

*Thunder.* Thunderstorms are frequent and are usually preceded by gusty squalls which continue during the earlier part of the storm. Except during squalls, winds of force 4 and 5 Beaufort scale are rare. Long violent storms never occur.

*Hail.* Hailstorms are not infrequent in Bunyoro but are so local that hail rarely falls more than twice in the year at any one place. Damage is caused to native crops, especially tobacco, and sometimes to young tree plantations on exposed sites. Within the forests, the overwood protects regeneration, and the storms are neither sufficiently severe nor the hailstones large enough to cause damage to mature trees.

*Humidity.* The humidity is not unduly high and mean values vary little from year to year (Table 4).

Table 4. *Mean percentage humidity of the air, and mean vapour pressure, at Butiaba, Masindi and Hoima, Bunyoro\**

Month	Mean percentage humidity of the air					Mean vapour pressure (mb.)†				
	Butiaba		Masindi		Hoima‡	Butiaba		Masindi		Hoima‡
	08.30 hr.	14.30 hr.	08.30 hr.	14.30 hr.		08.30 hr.	14.30 hr.	08.30 hr.	14.30 hr.	
Jan.	65	66	70	43	70	21.7	25.9	19.4	22.0	18.8
Feb.	65	67	66	42	68	22.0	26.3	17.3	16.0	18.5
Mar.	72	71	77	57	77	24.0	26.6	19.6	20.2	19.6
Apr.	73	71	80	60	79	24.5	*26.7	20.6	20.7	20.6
May	73	70	82	66	81	23.6	26.2	21.3	24.4	20.3
June	72	68	82	67	79	23.0	25.4	20.6	23.3	19.3
July	79	72	88	67	86	23.2	24.9	19.8	20.5	19.8
Aug.	78	73	85	65	87	23.5	25.3	20.0	20.7	20.1
Sept.	77	72	84	66	83	23.9	25.8	20.2	21.1	20.3
Oct.	77	73	81	62	81	24.3	26.0	20.8	20.3	20.8
Nov.	74	72	80	56	78	23.7	25.9	20.4	20.2	19.9
Dec.	72	69	77	54	75	23.0	25.4	19.3	18.8	19.7
Year	73	70	79	59	78	23.4	25.9	19.9	20.7	19.8

\* Altitudes are: Butiaba, 619 m. (2030 ft.), Masindi, 1146 m. (3760 ft.), Hoima, 1158 m. (3800 ft.).

† Butiaba and Masindi, years 1931–4; Hoima, years 1932–4.

‡ Readings at 08.30 hr. only.

*Vapour pressure.* Values over the District show typical variation with altitude (Table 4). Diurnal changes in pressure are slight. Mean figures for stations outside and inside the forest (years 1939–41) are given below:

Station	Vapour pressure (mb.)		
	08.30 hr.	14.30 hr.	Mean
No. 1. Outside the forest (control)	19.9	21.5	20.7
No. 2. Inside the forest (near S.P. 8)	21.9	22.6	22.3

*Evaporation.* Mean figures obtained outside and inside the forest (years 1939–41), using Piché tube evaprimeters, are:

Station	Inside the screen	Outside the screen
No. 1. Outside the forest (control)	3.1	4.1
No. 2. Inside the forest (near S.P. 8)	0.9	1.1

*Mist.* Mist usually rises from forested valleys where rain has fallen within half an hour of the evening showers which commonly occur between 17.30 and 18.30 hr. in the wet season. After prolonged evening rain these mist belts join, so that at dawn a mantle of mist is visible over the whole forest, disappearing rapidly as the sun rises.

*Sunshine.* Overcast periods are common around the forest. Days on which no sunshine is recorded are rare.

#### (4) *Biotic influences*

##### (i) *Man*

No large-scale destruction of closed forest has taken place in Bunyoro during the past 100 years, nor is there any evidence that extensive forest destruction by man has ever occurred. The land area of the District is approximately 1,243,000 ha. (4800 sq. miles), and the native population only about 100,000. Even if all poorly watered country unfit for settlement, and all sleeping sickness areas, forests and game reserves (amounting altogether to about one-third of the area of the District), are deducted from the total land area, the average density of population is still only about twelve persons per 100 ha. (about thirty-one to the square mile). Compared with most other parts of Uganda this is a low figure, and it is clear that Bunyoro is far from over-populated and that there is more than sufficient fertile, well-watered and easily worked land available for cultivation in the grasslands to make unnecessary the labour of felling and clearing forest. Moreover, although the population of Bunyoro is believed to have been much greater 100–150 years ago than it is now (it is known that inter-tribal wars and pestilence reduced it considerably about that time), yet in those days there were neither game reserves nor sleeping sickness areas, so that more land was available for occupation. For this reason, the average density of population is unlikely to have differed greatly from the figure of to-day.

Annually, in December and January, bush fires lighted by man devastate the grasslands which surround Budongo, searing and blackening the country up to the edge of the forest, where the flames peter out in the fringe of shrubby vegetation which in most parts protects the margin. There is no doubt that these fires slow down the expansion of the forest, especially in areas where the soil is poor, but it is most unlikely that any means will be found of stopping them. From the point of view of the forester it is in any case better that they should take place annually (and as early in the year as possible) rather than at irregular intervals when the accumulated dried grass of the years of non-burning adds to their ferocity. Further, although fire retards the expansion of the forest, it is by itself unable to stop the process.

In 1932, Budongo was gazetted an Undemarcated Forest, reserved to the Crown. Between 1911 and 1926, when the first sawmill was established, small quantities of timber were cut on the southern side of the forest, but the amount removed was negligible. From 1926 onwards there has been considerable exploitation by concession-holders operating in two concessions, one in the Siba forest and one in Budongo. Exploitation is strictly controlled by a Working Plan which ensures the rational exploitation of the forest and the replacement (by the Forest Department) of the trees which are felled. At the time of writing (1944) some 4100 ha. (16 sq. miles) of the forests have been exploited and the greater part of this area regenerated. The chief timbers cut are four African mahoganies (*Khaya anthotheca* C.DC., *Entandrophragma angolense* C.DC., *E. cylindricum* Sprague and *E. utile* Sprague), ironwood or muhimbi (*Cynometra alexandri* C. H. Wright), the two hardwoods mumara and muyati (*Erythrophleum guineense* G. Don and *Mildbraediodendron*

*excelsum* Harms.), the light hardwoods musizi, mujwa and musodo (*Maesopsis eminii* Engl., *Alstonia congensis* Engl. and *Ricinodendron africanum* Muell. Arg.), the iroko or muvule (*Chlorophora excelsa* Benth. & Hook. f.), Uganda mulberry or nyakatoma (*Morus lactea* Benth.), and African walnut or nkoba (*Lovoa brownii* Sprague).

Because felling is strictly controlled, and because replanting is undertaken so soon after felling, it is not expected that exploitation will for long affect materially the composition and appearance of the forest. Even so, to ensure the preservation of a small piece of virgin forest, an area of some 100 ha. (about 4 sq. miles) of easily accessible untouched forest has been set aside as a permanent Nature Reserve, where no interference with the vegetation is allowed.

## (ii) *Elephant*

Not without reason has Uganda been called 'Our Elephant Colony'. The Budongo forest alone is the headquarters of a herd estimated at 5000 head (Swynnerton, 1924). The presence of the animals constituting this claim to fame is not without its drawback, for it is undisputable that wherever they occur in numbers elephants are a limiting factor in the natural development of vegetation. On the Butiaba flats, below the Albert escarpment, elephants (and elephants only) prevent the present biotic (*bio-ecological*) climax of thicket-and-grassland from progressing to closed (probably evergreen) thicket and beyond. North, north-east and north-west of Budongo the same herd, in conjunction with fire, has likewise slowed down (and possibly now prohibits) the spread of the forest. Near Budongo in this area there are numerous high-forest nuclei (many of them based on streams) which are potential spawn for the spread of the forest. Around these nuclei the normal surrounding fringe of colonizing and protecting bush, which includes *Caloncoba schweinfurthii* Gilg and *Acanthus arboreus* Forsk. (E. 1460), is so battered and broken by elephants that dry-season fires penetrate to the edge of the forest, killing back all external colonizing regeneration and scorching the bases of the larger trees. In places, especially near favourite watering places, these forested patches are steadily decreasing in size. Owing to fire and elephants they are now relics rather than nuclei. Elephants, not fires, are the controlling factor.

Although not gazetted officially as a Sleeping Sickness Area (in its present form) till 1931, the grassland to the north and north-west of Budongo (i.e. between the forest and the Victoria Nile, and the forest and Lake Albert) has been closed to settlement since about 1912 when the entire population of the area was removed elsewhere on account of sleeping sickness. Since 1912, therefore, this tract together with the forest, has served the purpose of a Game Reserve. As long as the elephants remained within the boundaries of the reserve they were free from the molestation which they had suffered at the hand of man when the area was inhabited and when the increase of the herd was kept in check by the organized hunts necessary for the protection of the scattered settlements.

In practice, the animals made little use of the opportunity thus offered them for a peaceful existence and continued to maintain their old seasonal movements. The chief of these movements consisted of a regular annual emergence from the reserve in the Chopi area (east of Budongo) in June, a back and forth movement for some months thereafter along the Kafu river (or in the case of some of the animals, a movement between the reserve and Buruli), and a general return to the reserve in November. During its absence from the reserve the herd caused much damage to crops, but suffered in return only a



fraction of the punishment which it received prior to the coming of the European with his many restrictions on the hunting of game. The havoc caused by the herd became in fact so severe that it was one of the first aims of the Game Department (founded in 1925) to put a stop to the annual emergence, and to confine the herd permanently within the limits of the quadrangle bounded by the Victoria Nile, Lake Albert, and the Masindi-Matunda and Masindi-Butiaba roads. By constant patrolling and shooting during the danger months the Department has succeeded in this task, and in recent years the animals have made only slight efforts to leave the Reserve. Except from natural causes the herd is suffering little wastage and is increasing greatly in size. Swynnerton has estimated that even allowing for the loss from natural causes of half the progeny a herd can at least double its number in 30 years. If these figures are correct, the position clearly requires watching.

### (iii) *Tsetse*

The country to the west, north and north-east of Budongo has harboured tsetse-flies (*Glossina*) for at least three-quarters of a century. Flies of this genus have been termed 'foresters' friends' because by excluding man from large areas they thereby prevent the destruction of bush and forest. In the grasslands surrounding Budongo they have not had this effect. They have excluded man, whose actions were relatively harmless, and have encouraged elephants, whose actions are not.

### (iv) *Other factors*

So little is known of the influences of lesser biotic factors that it is only possible to indicate briefly some of the more obvious. Grassland termites build mounds which provide footholds for more advanced types of vegetation, these clumps acting in turn as centres for further spread. They may even, as suggested by Thomas (1942), control the distribution of certain trees, e.g. *Chlorophora*. Within the forests, as elsewhere, termites play an important part in breaking down dead plant matter; but may also destroy living growth. Other insects, which include gall-flies and shoot-borers, are usually regarded as pests; but many are pollinators. Rodents and small antelopes destroy fruits but, in so doing, disseminate the seeds. Birds, elephants, fruit-eating bats, chimpanzees, monkeys, civet cats and pigs do the same thing. Elephants break down saplings and are pests of regeneration areas; pigs root on the skirts of the forest and produce useful seed-beds; *Bombax reflexum* is pollinated by sun-birds. The list is endless, and biotic interaction so involved that it is almost impossible to interpret.

## III. GENERAL ACCOUNT OF THE VEGETATION

### (1) *Grassland*

Because Budongo is expanding, a short description must be given of the grassland at whose expense this is happening.

The forest is completely surrounded by grassland, with native cultivation nowhere extending to the forest's edge. In the western part of the tract, towards the top of the escarpment, the soil is poorer and the climate drier than elsewhere around the forest. For this reason the Biiso area has never been heavily settled. The grass growth here is less luxuriant than in the north and east, but low-statured trees are well distributed (Pl. 2, phot. 4). The two commonest trees are the small, red-fruited *Combretum binderanum*

Kotschy and the larger *Terminalia velutina* Rolfe, which attains 10 m. (35 ft.) and occasionally forms fairly dense stands. Other woody species include scattered specimens of the bush-like *Acacia stenocarpa* Hochst. ex A. Rich. (E. 447), one or two *Albizzias* (notably *A. coriaria* Welw.), *Bauhinia thonningii* Schumach., *Lannea barteri* Engl., *Stereospermum kunthianum* Cham. and *Vitex cuneata* Thonn. Small groups of *Acacia campylacantha* Hochst. ex A. Rich. and of *A. sieberiana* DC. are also found. A noticeable feature is the paucity of species.

On the small stony hills, typified by Busingiro (Pl. 3, phot. 5) and Little Kasenene, trees are considerably more abundant, and more species occur. All are deciduous. The commonest large trees are *Terminalia velutina* Rolfe, *Vitex cuneata* Thonn., *Combretum guenzii* Sond., *Lannea barteri* Engl., *Albizzia zygia* Macbride, *A. grandibracteata* Taub., *Entada abyssinica* Steud. and occasional *Pterocarpus abyssinicus* Hochst. ex A. Rich. Mixed with these are *Acacia stenocarpa* Hochst. ex A. Rich. (E. 447), *Annona chrysophylla* Boj., *Bridelia scleroneuroides* Pax, *Combretum binderanum* Kotschy, *Cussonia arborea* Hochst. ex A. Rich., *Erythrina abyssinica* Lam., *Grewia mollis* Juss., *Gymnosporia senegalensis* Loes., *Hymenocardia acida* Tul., *Psorospermum campestre* Engl., *Securidaca longipedunculata* Fresen., *Steganotaenia araliacea* Hochst. and *Stereospermum kunthianum* Cham.

These western grasslands are of the so-called 'short-grass' type. They show two distinct seasonal aspects. The grasses of the first aspect reach maturity 3–4 months after the annual burn and are, it is true, relatively short, attaining only 1–1.25 m. (3–4 ft.). Very soon, however, they become submerged and lost among the grasses of the second aspect, these latter reaching their maximum growth of 1.5–3 m. (5–10 ft.) in the late rains. In the first aspect, *Setaria sphacelata* Stapf & C. E. Hubbard (E. 4462) is usually the dominant grass, with *Brachiaria brizantha* Stapf (E. 4662) and *B. fulva* Stapf (E. 5318) very abundant to subdominant, and *Setaria longiseta* P. Beauv. (E. 4340) abundant. Other common species include *Paspalum commersonii* Lam. (E. 4294) and *Imperata cylindrica* Beauv. var. *thunbergii* Durand & Schinz (E. 4278), the latter especially common on the hills. Elephant grass, *Pennisetum purpureum* Schumach. (E. 4320), is not infrequent but is confined to patches of richer soil round termite hills where it is often associated with guinea grass, *Panicum maximum* Jacq. (E. 4315), which, however, is more catholic in its tastes and may form almost pure stands in valley-bottoms near streams.

By June or July the first (short grass) aspect is becoming smothered by the second which consists of a dense stand of *Hyparrhenias* in which *H. cymbaria* Stapf (E. 4578) is almost everywhere the dominant species. *H. rufa* Stapf (E. 4485), *H. diplandra* Stapf (E. 4284), and *H. schimperi* Anderss. (E. 4481) are commonly intermixed. *Andropogon gayanus* Kunth. var. (E. 5362), which attains 3.5 m. (12 ft.), and *Loudetia arundinacea* Steud. (E. 4358) are found amongst the *Hyparrhenias* on the hills. *Panicum maximum* Jacq. and *Pennisetum purpureum* Schumach. remain in possession of the richer patches of soil. In December, when the rains cease, this dense tangle of herbage dries quickly, requiring only a spark to set it alight and reduce it to ash.

North and north-east of Budongo the soil is richer, the climate wetter, and the grass growth correspondingly ranker than on the west. Trees are far less frequent, and are represented over wide stretches almost solely by old large specimens of *Terminalia velutina* Rolfe. Prior to the sleeping sickness evacuation, this area was in parts densely settled, and there is no doubt that human agency accounts for the scarcity of smaller trees and

that fire and elephants are responsible for maintaining this position. Guinea grass and elephant grass are both much more frequent on this side of the forest, and because of the more favourable conditions both these species (and also the *Hyparrhenias*) respond more quickly after the annual burn, with the result that the short grass aspect is not so marked a feature.

Between Masindi and Nyabea Hill and all down the eastern side of the Siba forest there are areas where the vegetation consists of an unbroken sheet of elephant grass 3–4 m. (10–13 ft.) high, extending up to the edges of the gulleys which contain the forest (Pl. 1, phot. 2).

The soil here is considerably deeper and more fertile than is usual in Bunyoro, so that these areas have for many generations undergone alternations of cultivation and fallow, which may account for the present complete cover of elephant grass. Partly owing to the density of the shade, and partly because of the intense root competition, trees are unable to establish themselves in pure stands of *Pennisetum*, and even where forest adjoins the elephant grass the position remains static, neither formation giving way to the other. In Uganda, pure stands of elephant grass usually indicate a man-made condition which persists, because of fire, even after man's activities have ceased. If burning can be prevented, the density of the stand diminishes, light enters, woody species regenerate and the slow process of forest formation begins.\*

## (2) *Forest*

Two main subdivisions of the African rain-forest formation can be recognized in Uganda, Upland Rain Forest and Lowland. Budongo, which belongs to the Lowland type, is in some respects intermediate between Rain Forest and Mixed Deciduous Forest as described from West Africa, but in structure and constituents, if not entirely climatically, it is typical Rain Forest.†

Aubréville (1936) states that the lower limit of rainfall for Evergreen Rain Forest on the Ivory Coast is 1600 mm. (63 in.), and Richards (1939) confirms that in south-western Nigeria, too, the boundary between the Mixed Deciduous Forest and the Rain Forest approximates with the isohyet of 1600 mm.

The mean annual rainfall on the outskirts of Budongo is slightly less than 1500 mm. (60 in.), but, as I have shown, the rainfall over the centre of the forest is probably at least 1780 mm. (70 in.).

\* The view expressed in Worthington (1938, p. 8) that 'in Uganda the large areas of elephant grass were once closed forest', has the support of Thomas (1940), who believes that 'elephant grass should be regarded as a man-made degradation of forest'. This is unquestionably true of Buganda and Bwamba, where man is still destroying closed forest and where all stages in its replacement by elephant grass can be seen. That it is equally true of the huge expanses of *Pennisetum* east of Ruwenzori, and of the elephant grass thickets of Bunyoro, is much less certain (cf. Michelmores, 1939, who is content to describe the former as 'perhaps secondary to forest'). In Bunyoro, as has been said, there is no evidence that man has ever cleared closed forest on a large scale. Here it is possible that the present-day stands of elephant grass indicate areas where well-wooded (*Terminalia*) grassland has been intensively farmed, with the result that the trees and short grass have gradually been replaced by *Pennisetum*.

Alternatively, it is possible that at the time when the original lateritic blanket over Bunyoro became eroded (see § II), elephant grass competed successfully with forest for the colonization of the freshly formed soils, and that with the aid of fire the grass has held its gains ever since.

† Rain Forest, as here understood, corresponds to the 'Tropical Semi-evergreen Rain Forest' of Burt Davy (1938). Mixed Deciduous Forest is his 'Moist Deciduous Forest'.

Richards (1939) has pointed out that in Nigeria the rainfall during the wet season must be more than adequate for the needs of vegetation everywhere in both the forest zones and that, contrary to expectation, the boundary between them is determined neither by the length of the dry season nor by the total rainfall during the dry months. He suggests the possibility that in Nigeria the dividing line between Rain Forest and Mixed Deciduous Forest is determined primarily not by the rainfall itself but by some factor correlated with it such as the distance inland reached by moist air from the sea during the dry season. The dry season at Budongo is less severe than at any of the Rain Forest stations for which Richards gives figures. Rainy days, too, are more numerous and better distributed (Table 5). This latter factor and the proximity to Budongo of two large bodies of inland water (Lake Albert on the west and Lake Kioga on the east) are probably important.

Table 5. *Rainfall and rainy days at Budongo, Uganda, and Akilla, Nigeria*

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean monthly rainfall (mm.):													
Budongo	23	77	129	188	173	134	98	155	153	160	132	73	1495
Akilla	28	35	96	180	196	407	419	134	252	242	80	11	2080
Mean no. of rainy days:													
Budongo	5 (3)	9 (7)	13 (11)	19 (16)	20 (16)	15 (11)	12 (10)	16 (15)	15 (15)	18 (16)	16 (14)	9 (7)	167 (141)
Akilla	1	3	8	9	13	18	17	13	18	16	8	1	125

Numbers in brackets indicate rainy days at Kyatarugo estate, 3.5 km. (2½ miles) from the edge of Budongo (years 1916-32 and 1939-42). Budongo figures (from the station at the Mile 55 Camp, Busingiro) cover the 10-year period August 1933-July 1943. The Akilla figures (from Richards, 1939) are for the years 1921-34.

*Chief types of forest.* At Budongo, in addition to Swamp Forest (edaphic climax), which is relatively unimportant, three main types of forest belonging to a single sere are recognized. They are Colonizing Forest (seral), Mixed Forest (seral), and Ironwood Forest (climatic climax). Colonizing Forest, the youngest type, occurs in two forms. In the first, Colonizing (*Maesopsis*) Forest, the dominant large tree is *Maesopsis eminii*; in the second, Colonizing (Woodland) Forest, *Maesopsis* is either absent or scarce. Mixed Forest is the mid-way stage in the development of Colonizing Forest to Ironwood Forest. It is the richest of the forest types and its canopy is composed of many species. In Ironwood Forest, *Cynometra alexandri* is dominant, forming over 75% of the canopy.

Mixed Forest (60%) and Ironwood Forest (32%) cover by far the great part of Budongo. Colonizing Forest accounts for a further 6% and Swamp Forest (2%) for the remainder.

*Colonization and succession.* Grassland and forest are normally separated, in Bunyoro, by a narrow belt of *Acanthus arboreus* Forsk. (E. 1460), a prickly shrub which attains 3.5 m. (12 ft.) in height. Around much of Budongo the forest is expanding and every year sees a few more yards won from the grassland. Expansion is most rapid in *Acanthus* areas, where reduced grass competition and lessened shade afford conditions suitable for the regeneration of *Maesopsis*, the principal tree colonizer. In such areas, *Maesopsis* Forest results.

Where *Acanthus* is absent, and especially on murram ridges and on patches of shallow soil, expansion is slower. Here *Albizia* spp., *Caloncoba schweinfurthii*, *Croton* spp., *Dombeya mukole*, *Olea welwitschii*, *Phyllanthus* spp., *Sapium ellipticum*, *Spathodea campanulata* and a few other species do most of the colonizing. By degrees they invade the grassland (usually first occupying the bases of termite mounds and thence spreading outwards),

partly kill out the grass, afford protection to undershrubs and herbs, and produce conditions which lead to the gradual formation of Woodland Forest.

The formation of *Maesopsis* Forest and Woodland Forest can be much hastened by fire protection. For this reason, bays of grassland lying between strips of gallery forest usually thicken very quickly. Fires in such areas are less fierce than elsewhere because the surrounding forest reduces fanning by wind.

*Maesopsis* Forest persists, as such, at Budongo, for only one generation. While the crop is young there is a regular distribution of age classes, but as the trees become older the smaller specimens become suppressed, the canopy thins, the lower stories and undergrowth thicken, *Maesopsis* fails to regenerate, and less violently light-demanding Mixed Forest species make their appearance.

The development of Woodland Forest to Mixed Forest is similar. Following the suppression of grass and the formation of a canopy, the stand of colonizers is gradually invaded by more truly forest species such as *Celtis* spp., *Funtumia* spp. and *Maba abyssinica*. There is a tendency for *Maesopsis*, too, to appear, but not in numbers.

The replacement of Mixed Forest by Ironwood Forest takes much longer than the preceding stage of the succession. The climax dominant (*Cynometra*) makes its first appearance before Mixed Forest reaches its optimum development, but its presence in the young stages is apt to be overlooked because it is not at first a fast-growing species and attention is captured by the more conspicuous saplings of light-demanders. By degrees, however, the ironwood becomes noticeable as it pushes its way through undergrowth and understory. It is catholic in its tastes and establishes itself everywhere. As more and more *Cynometra* appear, Mixed Forest species fail to regenerate, existing stems fall and are not replaced, and climax Ironwood Forest forms. The reason for the failure of Mixed Forest species to resist the invasion of the *Cynometra* is as yet imperfectly understood. Possibly they are unable to withstand the competition of its roots. The shade in Ironwood Forest is not unduly dense, and as a rule the purer the crop the thinner the undergrowth. There appears to be quite sufficient light for all but the most light-demanding of the Mixed Forest species, so that shade does not account, as was at first believed, for their failure to regenerate.

In Table 6 an attempt is made to indicate succession by listing the most abundant species in sample plots in the different types of forest. In Fig. 4 the instability of the seral types is expressed in graphical form.

*Spread.* An examination of the areas of Colonizing Forest shows conclusively that within the last thirty years Budongo has spread considerably. The evidence includes the presence of relict *Terminalia velutina* and of derelict termite mounds of a grassland type well within the forest, and is confirmed by a comparison of old and present-day maps.

To take a convenient example, Map 2 shows part of a recent stock-map of a portion of Budongo immediately north of Busingiro. Towards the top of the map is an area of Colonizing Forest known as Mpembeje. A typescript report (M.P. 67/32) in the files of the Uganda Forest Department states that in 1910, when the first survey of Budongo was made, the whole of this bay-like area was grassy. In the words of the writer (M. T. Dawe) the tree vegetation was 'mainly *Terminalia velutina*', the area being shown as grassland on the map accompanying the report. Air photographs taken in 1931 reveal that in that year no grass remained and that the whole bay had become closed forest.\*

\* For details of composition see Tables 10 and 11. S.P. 1 is situated almost in the centre of the bay; S.P. 2 in its south-west corner.

Table 6. Total number of individuals of species which are represented on three or more sample plots by four or more trees exceeding 20 cm. (8 in.) diam. (Swamp Forest excluded)

Maximum abundance in	Species	Colonizing (Woodland) Forest (S.P. 1)	Colonizing (Maesopsis) Forest (mean of S.P. 2 and 3)	Ecotone (S.P. 4)	Mixed Forest (mean of S.P. 5 and 6)	Ecotone (mean of S.P. 7 and 8)	Ironwood Forest (mean of S.P. 9 and 10)
Colonizing Forest	<i>Maesopsis eminii</i> Engl.	—	74	27	—	—	—
	<i>Olea welwitschii</i> Gilg & Schellenb.	48	54	31	—	—	—
	<i>Spathodea campanulata</i> Beauv.	23	10	4	—	—	—
	<i>Sapium ellipticum</i> Pax	14	12	8	—	—	—
	<i>Caloncoba schweinfurthii</i> Gilg	131	164	6	—	1	—
	<i>Phyllanthus discoideus</i> Muell. Arg.	19	32	32	1	1	—
	<i>Erythrophleum guineense</i> G. Don	15	15	5	2	1	—
Ecotone	<i>Funtumia</i> spp.*	1	32	104	20	23	—
Mixed Forest	<i>Trichilia prieuriana</i> A. Juss.	—	—	2	20	2	—
	<i>Alstonia congenis</i> Engl.	—	4	2	10	8	1
	Mahoganies†	—	—	2	15	7	1
	<i>Chrysophyllum</i> spp.‡	1	8	6	71	11	1
	<i>Celtis</i> spp.§	23	61	90	319	141	72
Ecotone	<i>Rinorea ardisiaeflora</i> O. Ktze.	—	—	5	13	70	27
Ironwood Forest	<i>Cynometra alexandri</i> C. H. Wright	—	—	—	36	55	119
	<i>Lasiodiscus mildbraedii</i> Engl.	—	—	—	—	118	258

\* *Funtumia elastica* Stapf; *F. latifolia* Stapf ex Schltr.

† *Entandrophragma cylindricum* Sprague; *E. utile* Sprague; *Khaya anthotheca* C.DC.

‡ *Chrysophyllum albidum* G. Don; *C. perpulchrum* Mildbr. ex Hutch. & J. M. Dalz.; *Chrysophyllum* n.sp.? (E. 2248).

§ *Celtis brownii* Rendle; *C. durandii* Engl. var. *ugandensis* Rendle; *C. soyauxii* Engl.; *C. zenkeri* Engl.

Similar evidence of the rapid expansion of Budongo is available for a number of other areas, and it is probable that the forest has been spreading for some time. The present proportions of the main types of forest bear out this view, since only a third of the forest is old enough to carry the climax type.

#### IV. METHODS: DESCRIPTION OF PLOTS

##### (1) Methods

Floristic composition was studied in eleven sample plots (S.P.), three situated in Colonizing Forest, two in Mixed Forest, two in Ironwood Forest, one in Swamp Forest, one in an ecotone between Colonizing Forest and Mixed Forest, and two in ecotones between Mixed Forest and Ironwood Forest.

Stratification was studied by means of four profile plots (P.P.), one in each of the two kinds of Colonizing Forest, one in Mixed Forest and one in Ironwood Forest.

The sample plots, 122 m. (400 ft.) square (= 1.418 ha. = 3.673 acres), were marked out by chain and compass. Each was divided into four strips 122 × 30.5 m. (400 × 100 ft.), and all trees over 10 cm. (4 in.) d.b.h. were measured, each strip recorded separately.\*

\* If sample plots are enumerated in strips, curves can be prepared showing the relationship between number of species and area within the plots. 'Each strip is treated as a separate unit, then by taking the average number of species on the four strips, on the six possible combinations of three strips, and the number on the whole plot, four points are obtained through which a species/area curve can be drawn' (Richards, 1939). In the case of S.P. 1, 2, 3, 8, 9 and 10, the curve was found to be flattening out at the area of the whole plot. In the case of S.P. 4, 5, 6 and 7 it was still rising slightly, and in the case of S.P. 11 (Swamp Forest) was rising steeply. For this latter plot alone, therefore, the area sampled was less than the 'minimal area' for trees 10 cm. (4 in.) diam. and over. Results are expressed in an abbreviated form in Fig. 5, where mean curves are shown for the various types of forest.

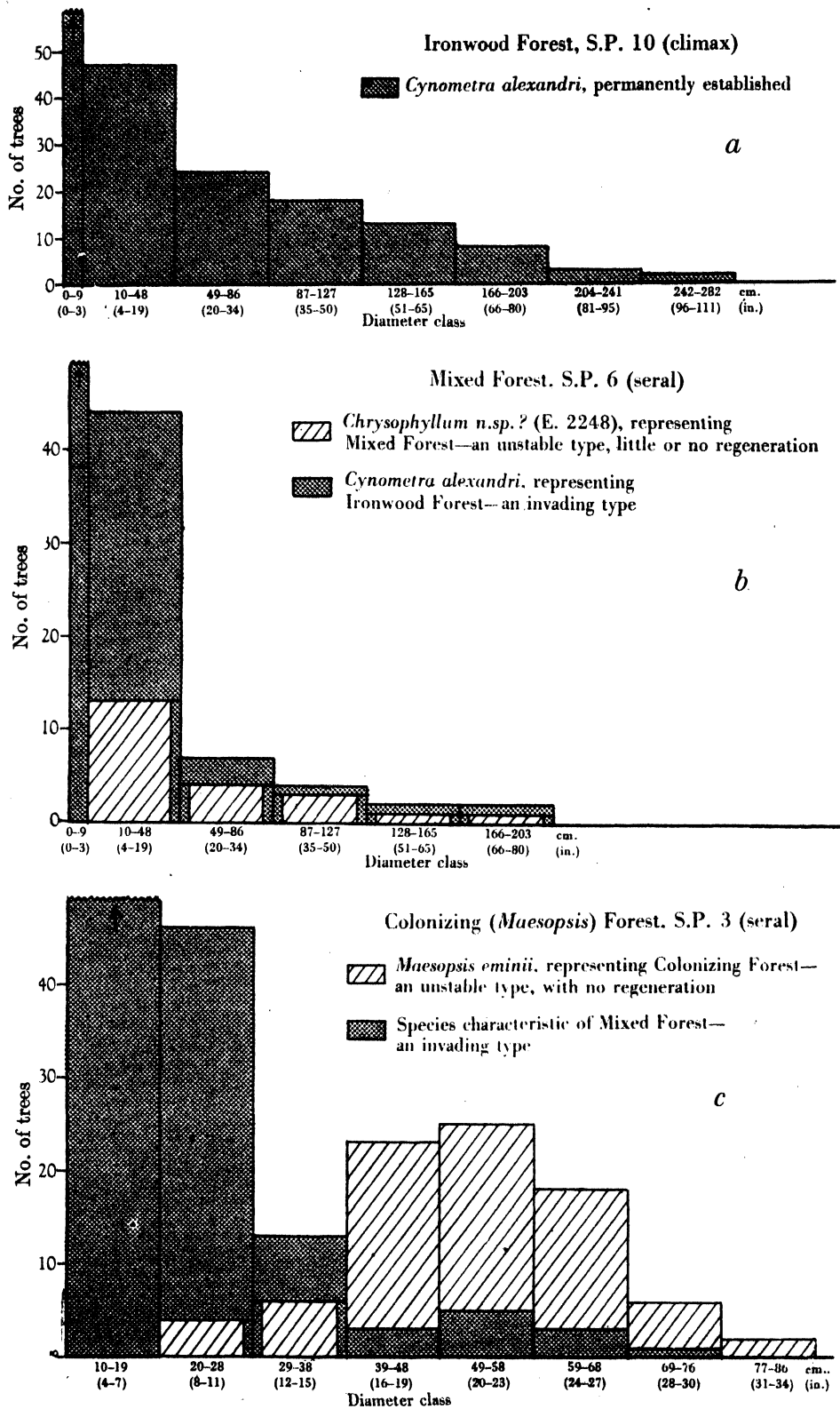
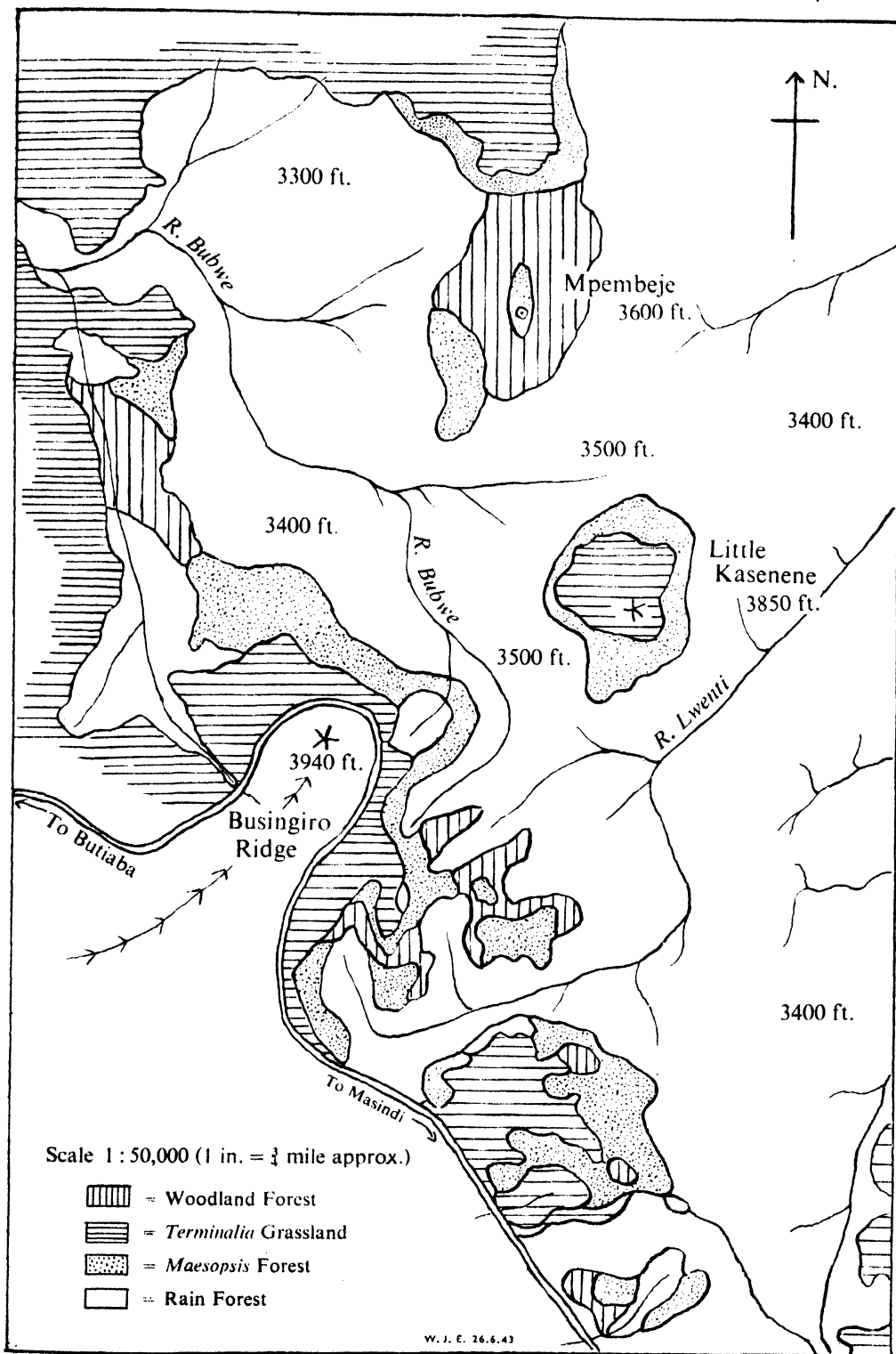


Fig. 4. Succession illustrated by graphs. Distribution of diameter classes of the most important trees in different types of forest.



Map. 2. Sketch-map of the west corner of the Budongo forest.



After the species and diameter of each tree had been noted its stem was at once blazed to prevent accidental remeasurement.

When all trees had been recorded, the abundance of the shrubs and herbs on the plot was assessed in general terms, using frequency symbols. The results are far from complete, but it is certain that all the more important species are listed. Notes were made also on lianas, climbers, epiphytes, parasites, saprophytes, and on the regeneration of timber trees. Soil pits were dug in representative areas in or near certain plots.

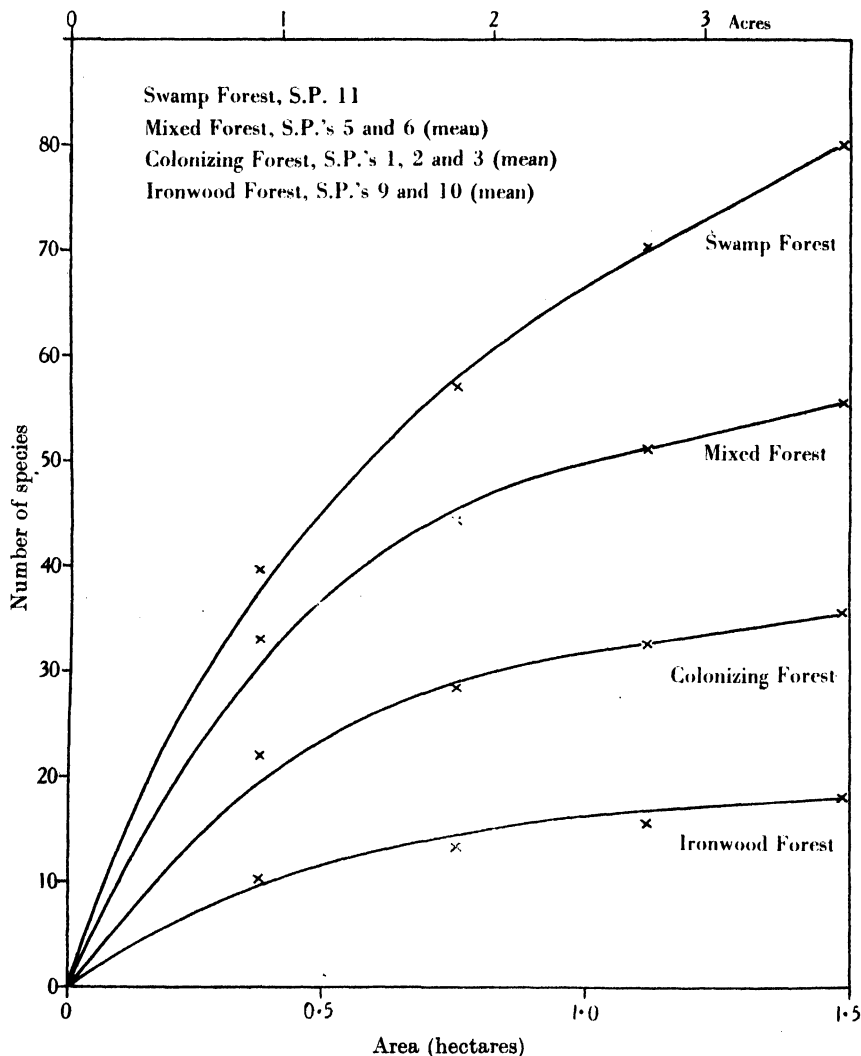


Fig. 5. Species/area curves for trees 10 cm. (4 in.) diameter and over.

The size of each of the four profile plots was 61 × 7.6 m. (200 × 25 ft.). All trees 4.6 m. (15 ft.) high and over on these plots were felled and measured.

The measurements included total height, height of lowest branch, height of lowest foliage, and width of crown; also diameter of stem at breast height, above buttress, and at crown collar. From the data thus obtained, the profile diagrams (Figs. 6–9) were prepared. The frequency and distribution of epiphytes were also recorded.

As a result of the experience gained in 10 years of botanical collecting at Budongo,

I was able to identify at sight practically all the plants encountered on the plots. Where there was the slightest doubt of identity the plant was gathered and matched against my reference collection of Budongo plants. Most of this collection was identified at Kew, where specimens have been deposited, but a few of the plants were determined at the East African Agricultural Research Institute at Amani. Duplicates of most of the numbers are available for study in Uganda, either in the herbarium of the Agricultural Department at Kawanda or in that of the Forest Department at Entebbe.

As far as trees are concerned, the names used and the taxonomic concepts which have been followed are those of my *Indigenous Trees of the Uganda Protectorate* (Eggeling, 1940*b*). For plants of this life-form I have quoted reference numbers in exceptional cases only, as when the exact specific identity is in doubt. The names of shrubs, herbs, climbers, etc. (for which no local flora yet exists), are coupled with my collecting numbers. The abbreviation (E.sn.) after a name indicates that the specimen in question has been named by matching against some other collector's material, such material having been named either at Kew or at the British Museum (Natural History).

## (2) Description of sample plots

S.P. 1. *Woodland Forest*. Near Mpembeje, 0.6 km. ( $\frac{1}{2}$  mile) north-east of S.P. 2. Age about 30 years. Practically level. Aspect south. *Olea welwitschii* the dominant large tree, forming 22% of stems 41 cm. (16 in.) diam. and over. *Caloncoba* dominant in understory, forming 31% of stems 10–40 cm. (4–15 in.) diam. Canopy very broken, few crowns meeting at the same level. Heights of adjoining large-diameter trees range from 12 m. (40 ft.), e.g. *Terminalia*, to 33 m. (110 ft.), e.g. *Olea*. Many relic *Terminalia velutina*. Many gaps. Shrub layer a confused intergrading of shrubs and small trees, the stratum better developed in canopy gaps than elsewhere. Herb layer very variable in density, wilting in dry weather. Shade very variable. Many disused grassland-type termite mounds.\* Litter sparse. Visibility (i.e. maximum distance at which a moving white-clad figure can be seen) 12–18 m. (40–60 ft.). Profile diagram, Fig. 6.

S.P. 2. *Maesopsis Forest*. Mpembeje, Biiso concession, on boundary between coupes 4 and 6. Age 30–40 years. Gently sloping side of low, wide, flat-topped ridge. Aspect west. *Maesopsis* the dominant large tree, forming 58% of stems 41 cm. (16 in.) diam. and over. Largest specimen 61 cm. (24 in.) diam. *Caloncoba* dominant in understory, forming 52% of stems 10–40 cm. (4–15 in.) diam. Canopy regular. Height about 30 m. (100 ft.). In 1940, the plot contained fourteen relic *Terminalia*; by 1943, only eight. Shrub layer very distinct. Herb layer uniform, not dense, wilting in the dry season when the ground dries and cracks and the *Maesopsis* become almost entirely leafless. Even light shade. Numerous disused grassland-type termite mounds. Good litter. Profile diagram, Fig. 7.

S.P. 3. *Maesopsis Forest*. Top of low ridge east of Sonso river, about 2 km. ( $1\frac{1}{2}$  miles) due east of S.P. 1. Age probably 50–60 years. Practically level, with sudden steep slope just outside south-east corner. *Maesopsis* the dominant large tree, forming 70% of stems 41 cm. (16 in.) diam. and over. Largest specimen 85 cm. (33 in.) diam. *Maba* dominant in understory, forming 22% of stems 10–40 cm. (4–15 in.) diam. Canopy level but many gaps between crowns. Height 27–30 m. (90–100 ft.). No relic *Terminalia*. Branchy undergrowth noticeably lacking, the lowest woody layer composed almost entirely of erect, single-stemmed shrubs and small trees with few branches below 1.8–2 m. (6–7 ft.). Visibility therefore long, often 21–24 m. (70–80 ft.). Herb layer regular, not dense, more litter than foliage visible. Shade even, medium-dense, cast chiefly by *Maba* and *Celtis brownii*. Numerous disused grassland-type termite mounds. Good litter. Topsoil markedly gravelly (ironstone particles). Soil pit 4.

S.P. 4. *Ecotone between Maesopsis Forest and Mixed Forest*. Lower south-west flank of Little Kasenene hill. Age varying from (probably) 60 to (at least) 150 years. Slope very gentle. Aspect south. North end of plot within 40 m. (45 yd.) of *Terminalia* grassland. Gradual transition from north to south from middle-aged *Maesopsis* forest to developing Mixed Forest containing a few sapling *Cynometra*. *Maesopsis* the dominant large tree especially at north end of plot, forming 31% of stems 41 cm. (16 in.) diam. and

\* The termite is *Bellicosus aurivillii* Sjost.

over. Largest specimen 126 cm. (50 in.) diam. Height of canopy, *Maesopsis*, *Olea* and *Pygeum* 27–33 m. (90–110 ft.), with large *Albizzia*, *Khaya* and *Piptadenia* in older portion of plot attaining 37 m. (130 ft.). *Trichilia heudelotii* (a Mixed Forest species) dominant in understory, forming 26% of stems 10–40 cm. (4–15 in.) diam. Well-spaced undergrowth to 6 m. (20 ft.), consisting chiefly of small trees. Shrubs, mostly with erect stems, scantily but regularly distributed. Herb layer very uniform—an almost complete cover of *Leptaspis cochleata*. Irregularities of canopy not reflected on undergrowth and soil cover owing to uniform shade cast by numerous well-grown *Funtumia latifolia*, and regular understory. Shade even, medium-dense. Visibility about 18 m. (60 ft.). Grassland-type termite mounds not prominent, those present much flattened and difficult to distinguish. Good litter, well decayed.

S.P. 5. *Mixed Forest*. Between Busingiro and Little Kasenene hills, east of Bubwe streamlet. Age unknown, possibly 200–250 years. Gentle slope, steeper towards south. Aspect south-west. No dominant large tree. *Chrysophyllum* n.sp.? (E. 2248) the commonest species 41 cm. (16 in.) diam. and over (nine individuals), followed by *Alstonia congensis* and *Trichilia prieuriana* (eight each). The genus *Chrysophyllum* (*C. albidum*, *C. perpulchrum*, and *Chrysophyllum* n.sp.?) with eighteen individuals, forms 23% of stems 41 cm. (16 in.) diam. and over. Five large mahoganies (three *Entandrophragma cylindricum*; two *Khaya anthotheca*) occur. *Celtis soyauxii* dominant in understory, forming 33% of stems 10–40 cm. (4–15 in.) diam. Canopy reasonably regular, 40–46 m. (130–150 ft.) high, but many emergent trees, the tallest 55 m. (180 ft.). Upper limit of lowest woody layer well defined but herbs, shrubs and small trees merge and mingle. Visibility about 13 m. (45 ft.). *Leptaspis cochleata* the dominant herb. More humus than foliage visible. Shade dense. Remains of grassland-type termite mounds difficult to distinguish. A few nests of tree termites (*Microcerotermes edentatus* Wasm.). Much surface humus. Loose rocks of decomposed granitic gneiss in south-west corner. Profile diagram, Fig. 8.

S.P. 6. *Mixed Forest*. Near source of Bubwe streamlet, due east of Budongo Forest Station. Age unknown (older than S.P. 5). Stream crosses plot from south to north. Stream-bed flat, stony, 3–4 m. (10–14 ft.) wide. East and west boundaries of plot about 12 m. (40 ft.) above valley bottom. Slope slight to medium on eastern and western boundaries, becoming very steep near stream. *Cynometra* the commonest large tree, forming 24% of stems 41 cm. (16 in.) diam. and over, only just exceeded (25%) by three species of *Chrysophyllum* (*C. albidum*, *C. perpulchrum* and *Chrysophyllum* n.sp.?) taken together. Nineteen large mahoganies (two *Entandrophragma cylindricum*; one *E. utile*; sixteen *Khaya anthotheca*). *Celtis soyauxii* dominant in understory, forming 42% of stems 10–40 cm. (4–15 in.) diam. Canopy irregular owing to presence of many emergent large trees (especially mahogany) and to several gaps. Average height 40–43 m. (130–140 ft.), emergent individuals attaining 49–52 m. (160–170 ft.). Upper limit of shrub layer well defined, determined chiefly by *Rinorea poggei*. Visibility about 12–15 m. (40–50 ft.). Herb layer thin, *Leptaspis cochleata* the commonest species. Much more humus than foliage visible. Ferns more abundant than usual in herb layer because of proximity of water; dicotyledons poorly represented. Lianas plentiful. Practically no trace of grassland-type termite mounds but many shafts (with protruding pipe-like entrances) of a forest termite (probably a small species of *Termes*). Shade medium to dense. Litter abundant. Humus dry and powdery.

S.P. 7. *Ecotone between Mixed Forest and Ironwood Forest*. East of Kamirambwa river in Nature Reserve. Age unknown. Almost level; very gentle slope towards river about 200 m. (660 ft.) distant. Aspect west. *Cynometra* the dominant large tree, forming 43% of stems 41 cm. (16 in.) diam. and over. Mixed Forest species still well represented with a total of twenty-four large *Alstonia*, *Chrysophyllum*, *Entandrophragma* and *Khaya* as against thirty large *Cynometra*, *Lasiodiscus* dominant in understory, forming 37% of stems 10–40 cm. (4–15 in.) diam. Height of canopy about 46 m. (150 ft.), with emergent individuals to 55 m. (180 ft.). Many gaps in canopy due to recent windfalls of *Khaya* and *Entandrophragma*. The *Cynometra* in the largest diameter class mostly only part-grown and tendency for these to spread into gaps. Many trees in lowest diameter class attain 9–15 m. (30–50 ft.), e.g. *Celtis soyauxii* and *Rinorea ardisiaeflora*. Layering not marked below this height, because shrubs and small trees intermingle. Undergrowth relatively open at eye level, i.e. little branching below 2 m. (6 ft.). Herb layer uniform except in gap tangles; *Leptaspis* dominant. Shade medium-dense. Visibility about 18 m. (60 ft.). No sign of termite mounds of grassland type. A few shafts of *Cubitermes* sp. Litter plentiful. Soil pit 2.

S.P. 8. *Ecotone between Mixed Forest and Ironwood Forest*. Near boundary between coupes 4 and 5, Siba concession. Age unknown. Aspect north. *Cynometra* the dominant large tree, forming 64% of stems 41 cm. (16 in.) diam. and over; *Lasiodiscus* dominant in understory forming 46% of stems 10–40 cm.

(4–15 in.) diam. Top-story trees all much the same height, with few emergent individuals, but many gaps where old trees (chiefly mahoganies and ironwood) have fallen. Height 40–46 m. (130–150 ft.). All sizes of *Cynometra* well represented. Lowest woody layer well developed, individual *Celtis brownii* (21.3 m. = 70 ft.) and *Rinorea ardisiaeflora* (10.7 m. = 35 ft.) attaining larger size than usual. Shrub layer variable, individuals rather widely spaced except in gaps. Visibility 18–21 m. (60–70 ft.). Herb layer regular. Much more humus than foliage visible. No sign of grassland-type termite mounds. Numerous pipe-shafts of *Cubitermes* sp. Shade even, not dense. Litter thin, uniform, composed chiefly of *Cynometra* leaflets. Humus powdery. Soil pit 1.

S.P. 9. *Ironwood Forest*. Lower slopes of Kasenene ridge about 4 km. (2½ miles) north-east of Nyabea hill. Age unknown. Very gentle north-west slope. *Cynometra* the dominant large tree, forming 76% of stems 41 cm. (16 in.) diam. and over. *Lasiodiscus* dominant in understory, forming 62% of stems 10–40 cm. (4–15 in.) diam. Canopy thin; very regular except for occasional gaps caused by fall of old trees. Height about 40 m. (130 ft.). Few emergent individuals. Shade light. Unusually good growth of *Celtis soyauxii* and *Lasiodiscus mildbraedii*, the former contributing materially to the top story, the latter attaining 15 m. (50 ft.). Shrub layer very distinct; height 2.4–4.6 m. (8–15 ft.). Undershubs poorly represented, hence long visibility of 30–45 m. (100–150 ft.). Herb layer regular, rather thin, much more litter than foliage visible. Lianas rare. No sign of grassland-type termite mounds but small castles of a forest termite (*Cubitermes ugandensis* Fuller) frequent in angles of buttresses. Many elephant paths. Good litter of *Cynometra* leaflets, with dry powdery humus below. Topsoil dark brown, about 23 cm. (9 in.) deep. Subsoil bright red, about 46 cm. (18 in.) thick, over decomposing shale containing quartz stringers.

S.P. 10. *Ironwood Forest*. East bank of Sonso river, about 360 m. (400 yd.) from forest edge. Age unknown. Gentle slope between ridge (carrying Colonizing Forest) and river. Aspect west. *Cynometra* the dominant large tree, forming 85% of stems 41 cm. (16 in.) diam. and over. *Lepidoturus* dominant in understory, forming 29% of stems 10–40 cm. (4–15 in.) diam. Canopy regular, except where old trees have fallen. Height 40–46 m. (130–150 ft.). Well-defined shrub layer, 1.8–3.6 m. (6–12 ft.) high with larger *Lepidoturus* growing through. Layer lower, more branched, and denser than normal, due to elephants. Herb layer mainly seasonal. Plot interlaced with tracks made by elephants which frequent it in the hot weather. In the rains these paths bear a dense crop of herbs (chiefly *Brillantaisia*) which almost disappear in the dry season. Shade even, not dense. No sign of grassland-type termite mounds. Litter thin but uniform, composed of the leaflets and pods of *Cynometra*. Humus powdery.

S.P. 11. *Swamp Forest*. Stream-side forest on tributary of Kanyege stream near mile-post 53 on the Masindi Port-Butiaba road. Age unknown. Forest strip little wider than plot. Drainage south-east to north-west, imperceptible. Ground permanently waterlogged, but little visible water except in wet weather. North, west and north-west sides of plot slightly higher, and hence drier, than remainder. *Mitragyna* dominant both in overwood and underwood, forming 21% of stems 41 cm. (16 in.) diam. and over, and 15% of stems 10–40 cm. (4–15 in.) diam. *Mitragyna* canopy fairly regular in height, averaging about 30 m. (100 ft.), with emergent individuals to 33 m. (110 ft.). On drier sides of plot other species attain 43 m. (140 ft.) or more. *Mitragyna* apart, *Funtumia latifolia* the only common middle-story tree in the wetter areas. Small trees noticeably deficient. Many *Khaya* saplings. Woody undergrowth very scanty, *Dracaena laxissima* characteristic. Rattan (*Calamus*) ubiquitous, climbing almost every medium-sized and large tree. Lianas and epiphytic figs abundant. Herb growth monocotyledonous; *Marantochloa* dominant. Shade even, mostly very light. Visibility long, often 30 m. (100 ft.). Soil accumulations at base of many old trees (probably due to termites). Many mounds of the termite *Cubitermes ugandensis* Fuller built against bases of trees in wetter parts. Shafts of a second (subterranean) species of termite (*Termes badius* Hav.) noticeable on drier patches. Much vegetable matter on soil surface. Deep humus.

### (3) Description of profile plots\*

P.P. 1. *Woodland Forest*. Situated in S.P. 1. The plot contained sixty-three trees, only one of which (1.4%) bore epiphytes. Scarcity of lichens and ferns remarkable. No parasites. No lianas, but seven species of climbers, represented by twenty-three individuals. Of these, five species (sixteen individuals) never exceeded 7.5 m. (25 ft.). The remaining two species (both Hippocrateas) attained 12.2 m. (40 ft.). *Popowia littoralis* Bagsh. & Bak. f. (E. 2003) was the only climber determined specifically.

\* Only in the case of Woodland Forest could a sample plot be used for profile purposes. The plots in other types are permanent sample plots of the Uganda Forest Department and could not be felled.

P.P. 2. *Maesopsis Forest*. Situated alongside S.P. 2. The plot contained sixty-nine trees, eight of which (11.7%) bore epiphytes. No parasites. No lianas, but thirty-nine species of climbers, represented by eighty-one individuals. Of these, twenty-six species (forty individuals) never exceeded 7 m. (23 ft.); and ten species (thirty-six individuals) never exceeded 15 m. (50 ft.). The remaining three species (five individuals) attained 15–24 m. (50–80 ft.). Climbers present included:

(i) Small climbers not exceeding 7 m. (23 ft.): *Abrus* sp. (E.sn.), *Afromendoncia gilgiana* Lindau (E.sn.), *Artabotrys nitidus* Engl. (E. 431), *Clerodendron capitatum* Schum. & Thonn. (E.sn.), *Hippocratea* sp. (E.sn.), *Ipomoea* sp., *Paullinia pinnata* Poir. (E. 140), *Rutidea smithii* Hiern (E. 33), *Secamone platystigma* K. Schum. (E. 4063) and *Tetracera potatoria* Afz. (E. 450).

(ii) Tall climbers not exceeding 15 m. (50 ft.): *Abrus pulchellus* Wall (E.sn.), *Cissus dubia* Becc. (E.sn.), *Clerodendron* sp. (E.sn.), *Combretum rhodanthum* Engl. & Diels (E. 1602), *Ipomoea* sp., *Popowia littoralis* Bagn. & Bak. f. (E. 2003) and *Tragia brevipes* Baker (E. 56).

(iii) Tall climbers, attaining 15–24 m. (50–80 ft.): *Buettneria africana* Mast. (E. 3835).

P.P. 3. *Mixed Forest*. Situated alongside S.P. 5. The plot contained sixty-seven trees, eleven of which (16.3%) bore epiphytes. There were two tufts (two species) of *Loranthus* (hemi-parasite). Altogether eleven species (fifteen individuals) of climbers and lianas. Of these, four species (five individuals), none of which was identified, never exceeded 7 m. (23 ft.). The remaining seven species (ten individuals) attained 12–24 m. (40–80 ft.). They included *Barleria brownei* S. Moore (E. 2304), *Canthium* sp. (E.sn.), *Dichapetalum ugandense* M. B. Moss (E. 1147), *Hippocratea* sp.; *Pisonea aculeata* Linn. (E.sn.) and *Uncaria africana* G. Don (E. 3733). No attempt was made to identify herbs and shrubs of which there were at least twenty-nine species less than 1 m. (3 ft.) high, and at least fifty-one species 1–4.5 m. (3–15 ft. high).

P.P. 4. *Ironwood Forest*. Situated about 275 m. (900 ft.) north-east of S.P. 8 in Ironwood Forest approaching climax development. The plot contained forty-four trees, ten of which (22.7%) bore epiphytes. No parasites. Altogether five species (eight individuals) of creepers and small lianas. Of these, three species (five individuals), of which two were Hippocrateas, did not exceed 8 m. (26 ft.). The other two species (three individuals), one of which was *Dichapetalum ugandense* M. B. Moss (E. 1147), attained 15–18 m. (50–60 ft.).

## V. STRUCTURE OF THE FOREST TYPES

### (1) *Stratification of the trees*

*Woodland Forest* (P.P. 1, Fig. 6) is two-storied. There is: (i) a medium-dense to dense bottom story of trees up to about 21 m. (70 ft.) high, forming an almost closed lower canopy but with small gaps here and there, and (ii) a very irregular emergent top story of larger trees. The crowns of these top-story trees are not normally in lateral contact, i.e. the upper canopy is not closed.

Of the fifty-seven trees less than 21 m. (70 ft.) high in P.P. 1 only five are young individuals of taller trees, the remaining fifty-two trees of twelve species belonging to the story. The tallest emergent tree in P.P. 1 is 32 m. (105 ft.) high.

From the diagram it looks as if the bottom story, as defined above, should be divided into two, namely, into a lower stratum up to 9 m. (30 ft.) high, and a higher stratum 9–21 m. (30–70 ft.) high. The figures for P.P. 1 show, however, that of the forty-two individuals less than 9 m. (30 ft.) high only ten, belonging to five species, are not young individuals of taller trees, and that of these ten the majority are simply well-grown specimens of the shrub layer (not shown in diagram).

Of the five species (six individuals) which form the top story in P.P. 1 only two (*Morus* and *Phyllanthus*) are at all common in the next stage of the succession. There are saplings of both species in the understory of the plot. The other three top-story species (*Croton*, *Olea* and *Spathodea*) are pioneers. Like *Caloncoba* (the pioneer understory colonizer) they have ceased to regenerate. Typical Mixed Forest species already present as young

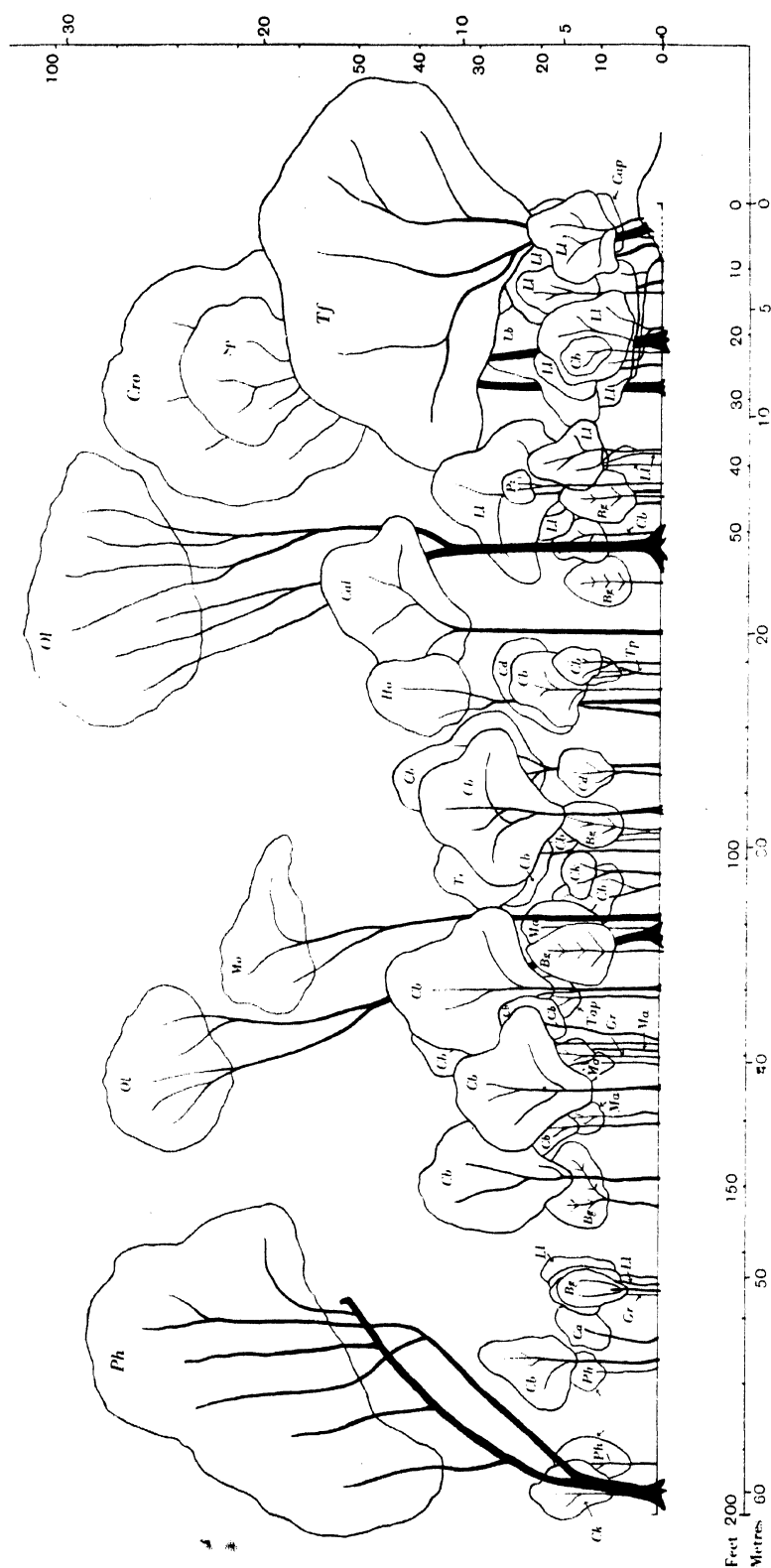


Fig. 6. Profile diagram of Woodland Forest, Budongo. The diagram represents a strip of forest 61 m. (200 ft.) long and 7.6 m. (25 ft.) wide. The following are based on measurements and drawn strictly to scale: position, diameter at breast height, total height, height to first branch, lower limit and spread of crown. It has been necessary as a convention to draw the crowns compact and dense (very rarely the case). The plot contained sixty-three trees 4.6 m. (15 ft.) high and over. All are shown.

Figs. 6-9. **Key to symbols.** *Ac*, *Alstonia congenisis*; *Bg*, *Belonophora glomerata*; *Ca*, *Chrysophyllum albidum*; *Cal*, *Caloncoba schweinfurthii*; *Cap*, *Capparis afzelii*; *Cb*, *Celtis brownii*; *Cd*, *Celtis durandii* var. *ugandensis*; *Ceu*, *Coffea eugenoides*; *Ch*, *Conopharyngia holstii*; *Chn*, *Chrysophyllum* n. sp.?; *Ck*, *Celtis kraussiana*; *Cn*, *Clausena anisata*; *Cp*, *Chrysophyllum perpulchrum*; *Cro*, *Croton macrostachys*; *Cs*, *Celtis sogaurii*; *Cr*, *Canthium vulgare*; *Cyn*, *Cynometra alexandri*; *Cz*, *Celtis Zenkeri*; *Dm*, *Drypetes ugandensis*; *Eh*, *Ehretia cymosa*; *Er*, *Erythrophloeum guineense*; *Eu*, *Euphorbia leke*; *Fl*, *Funtumia latifolia*; *Fm*, *Fagaria melanacantha*; *Fu*, *Funtumia elastica*; *Gc*, *Guarea cedrata*; *Gr*, *Grewia pubescens*; *Ho*, *Holoptelea grandis*; *Kg*, *Klainedoxa gabonensis*; *Kh*, *Khaya anthotheca*; *Ll*, *Lepidolurum lariflorus*; *Lm*, *Lasiodiscus mildbraedii*; *Ma*, *Maba abyssinica*; *Me*, *Maesopsis eminii*; *Ml*, *Mildbraediodendron excelsum*; *Mo*, *Morus lactea*; *My*, *Myrianthus arboreus*; *Od*, *Ouratea densiflora*; *Ol*, *Olea velutina*; *Ph*, *Phyllanthus discoides*; *Pi*, *Pavetta insignis*; *Ra*, *Rinorea ardisiaeflora*; *Rp*, *Rinorea poggei*; *Rv*, *Rauvolfia vomitoria*; *Sa*, *Sapium ellipticum*; *Sp*, *Spathodea campanulata*; *Tap*, *Tapura fischeri*; *Te*, *Teclea nobilis*; *Tf*, *Truraea floribunda*; *Tm*, *Terminalia velutina*; *Tr*, *Trichilia prieuriana*; *Us*, *Uvaropsis* n.sp. (E. 2291).

individuals in the bottom story include *Chrysophyllum albidum*, *Holoptelea grandis* and three species of *Celtis*.

It can be seen from the profile diagram that the smaller trees in Woodland Forest tend to be grouped around the larger, i.e. that colonization proceeds outwards from suitable centres. At the right-hand end of the profile the clustering of the trees round an abandoned termite mound illustrates the important part played by sites of this nature in the early stages of colonization, due chiefly to the more favourable soil conditions (including the local accumulation of bases) caused by the activities of the termites.

*Maesopsis Forest* (P.P. 2, Fig. 7) resembles Woodland Forest in stratification, but has a much more regular top story. There are: (i) a medium-dense to dense bottom story of trees up to about 21 m. (70 ft.) high, forming a closed lower canopy, and (ii) a remarkably even top story 21–30 m. (70–100 ft.) high, forming a practically closed upper canopy. Of the sixty-three trees less than 21 m. (70 ft.) high in P.P. 2 only four are young individuals of taller trees, the remaining fifty-eight of fourteen species (the single *Terminalia* excepted) being true bottom-story species. In this profile, as in that of Woodland Forest, there is a temptation to subdivide the bottom story into two. The data from P.P. 2 show, however, that of the fifty-four trees less than 9 m. (30 ft.) high which occur in the plot only twenty-eight of eight species are not immature individuals of taller trees, and that the majority of these are only well-grown shrubs. Of the six trees 9–21 m. (30–70 ft.) high (the *Terminalia* again disregarded) no fewer than five are *Caloncoba*, once more emphasizing the importance of this species as a bottom-story colonizer. As in the case of P.P. 1 the influence of abandoned termite mounds is noticeable (left centre of diagram). A constant feature of *Maesopsis Forest* is the umbrella-shaped crown of the dominant. Relic *Terminalia velutina* (one visible in diagram) testify to the rapidity of formation of this type of forest under favourable conditions. As stated on p. 38, it is only thirty years since P.P. 2 formed part of a grassland area where the only trees were scattered *Terminalia* and perhaps a few young *Maesopsis*.

*Mixed Forest* (P.P. 3, Fig. 8) differs from Colonizing Forest in having four stories, as follows: (i) a fairly dense bottom story of small trees up to about 11 m. (35 ft.) high, forming a closed canopy except (sometimes) under the largest trees of the overwood. The crowns of these small trees are usually rounded or broadly pyramidal. Of the forty-six trees in this layer in P.P. 3, fifteen are young individuals of taller trees, the remaining thirty-one of nine species belonging truly to the story. Above the lowest stratum there is (ii) a regular second story of trees about 11–21 m. (35–70 ft.) high, whose usually oblong crowns are generally in lateral contact. This story and the bottom story always form, in conjunction, a closed (lower) canopy. In P.P. 3 the second story contains twelve trees of five species. Three of these trees, each a different species, are immature specimens of taller trees. Above the second story there is an irregular mass of trees which according to observations made over the whole of S.P. 5 and elsewhere can be divided into (iii) a third story about 21–36 m. (70–120 ft.) high, and (iv) a fourth (top) emergent story 36 m. (120 ft.) high and upwards. The tallest emergent tree in P.P. 3 is 42 m. (138 ft.) high, but a nearby *Entandrophragma cylindricum* measured 55 m. (180 ft.). Taken together, the two top layers form a closed (upper) canopy: individually they do not.

In P.P. 3 there are three trees in the emergent story, an unusually high number for the area involved. None of these three trees is particularly large and all have smaller crowns than usual. The presence of three emergent trees in so limited an area has had its effect





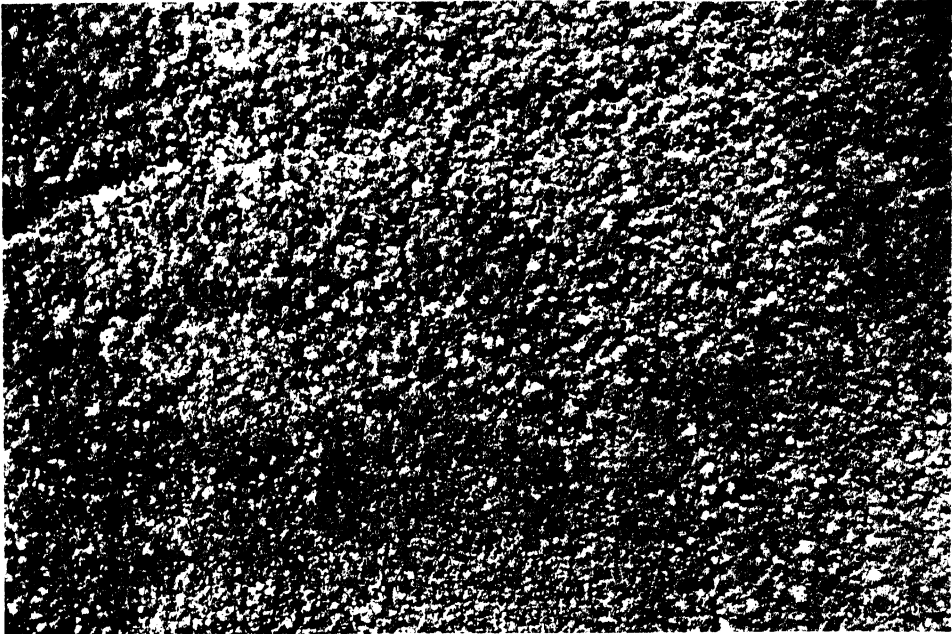


Phot. 1. View over Budongo from Busingiro hill, with Little Kasenene hill at left background. The white-stemmed trees are *Macsopsis emini* Engl. Phot. by A. S. Thomas.



Phot. 2. Aerial view showing gallery forest and stands of elephant grass (*Pennisetum purpureum* Schumach.), Siba area. The forest is not spreading, its edge sharply defined. There are practically no trees in the elephant grass. Bush sawmill top right.

Phot. by Air Survey Company Ltd., London.



Phot. 3. Aerial view of *Macsopsis* forest (lower) and mixed forest (upper), Budongo. The picture shows very clearly the level canopy of the former type and the numerous emergent trees of the latter.

*Phot. by Air Survey Company Ltd., London.*

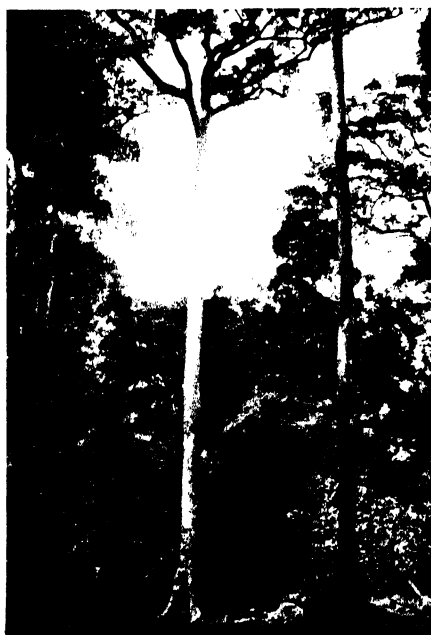


Phot. 4. Aerial view of part of the margin of Budongo in the Nyakabiiso area, where the forest is spreading. The grassland is of the 'short-grass' type and contains numerous trees, chiefly *Terminalia velutina* Rolfe.

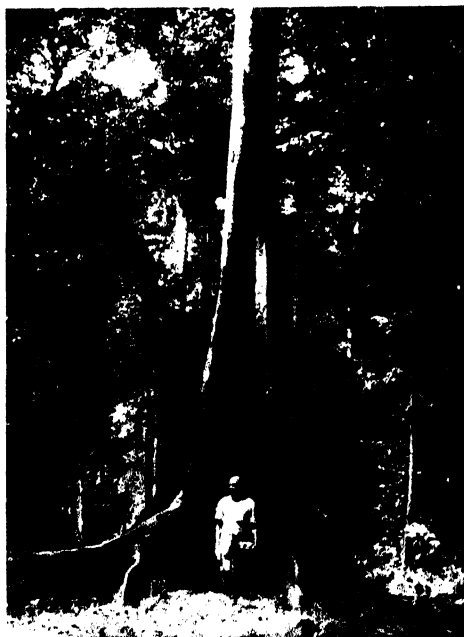
*Phot. by Air Survey Company Ltd., London.*



Phot. 5. Grassland with trees, Busingiro hill. *Lannea barteri* Engl. on left; *Combretum* spp., *Terminalia velutina* Rolfe, and other trees in centre and on right.



Phot. 6. *Entandrophragma cylindricum* Sprague showing typical habit of an emergent tree in mixed forest. The bole measured 31.7 m. (104 ft.) from ground level to crown collar. Note the thick buttresses.



Phot. 7. Young ironwood (*Cynometra alexandri* C. H. Wright) showing early development of plank buttresses.

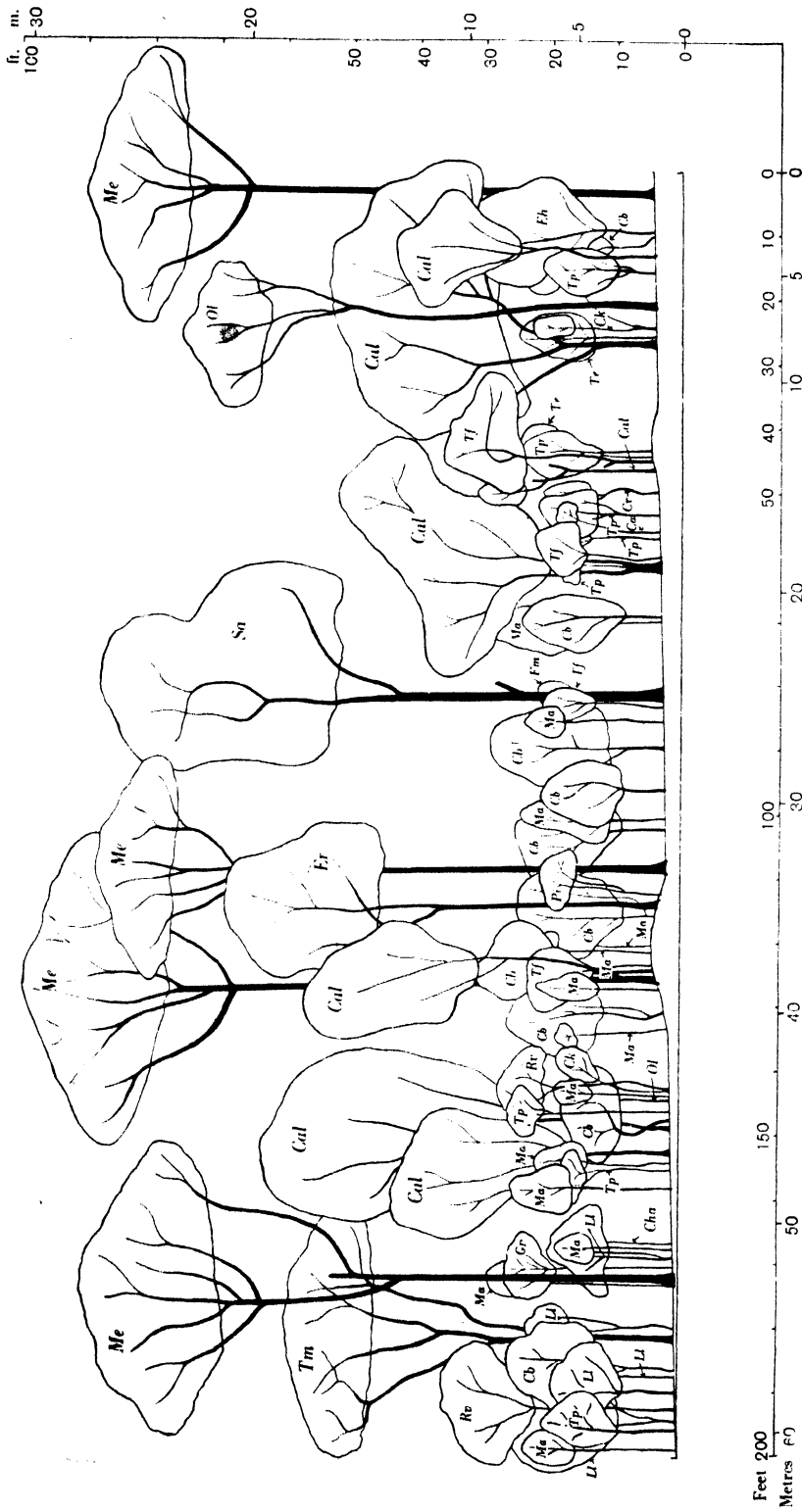


Fig. 7. Profile diagram of *Maesopsis* Forest, Budongo. The diagram represents a strip of forest 61 m. (200 ft.) long and 7.6 m. (25 ft.) wide. The following are based on measurements and drawn strictly to scale: position, diameter at breast height, total height, height to first branch, lower limit and spread of crown. It has been necessary as a convention to draw the crowns compact and dense (very rarely the case). The plot contained sixty-nine trees 4.6 m. (15 ft.) high and over. All are shown.

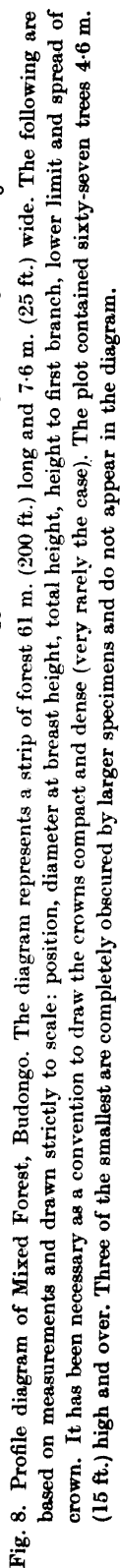


Fig. 8. Profile diagram of Mixed Forest, Budongo. The diagram represents a strip of forest 61 m. (200 ft.) long and 7.6 m. (25 ft.) wide. The following are based on measurements and drawn strictly to scale: position, diameter at breast height, total height, height to first branch, lower limit and spread of crown. It has been necessary as a convention to draw the crowns compact and dense (very rarely the case). The plot contained sixty-seven trees 4-6 m. (15 ft.) high and over. Three of the smallest are completely obscured by larger specimens and do not appear in the diagram.

on the third story, which is poorly developed. The height of the third story is normally determined chiefly by *Chrysophyllum* spp. Only young specimens of *Chrysophyllum* occur in P.P. 3, although a mature individual can be seen to the extreme left of the diagram just outside the plot.

From observations made over Budongo as a whole it was found that mahoganies (genera *Khaya* and *Entandrophragma*) are the commonest emergent trees in Mixed Forest, that emergent *Klainedoxa* and *Mildbraediodendron* are frequent, and that emergent specimens of *Chrysophyllum* n.sp.? (E. 2248) and of *Alstonia* are not uncommon. Only one young individual of any of these trees is represented in the lower layers of P.P. 3, where the presence of an ironwood sapling shows that the invasion of Mixed Forest by *Cynometra* has already begun.

*Ironwood Forest* (P.P. 4, Fig. 9). The only difference between the stratification of Mixed Forest and Ironwood Forest lies in the fact that in the former the emergent layer is composed of species different from those of the layer immediately beneath it, whereas in Ironwood Forest the emergent trees are simply exceptionally well-developed specimens of *Cynometra*, the species which dominates the main layer. The emergent trees of Ironwood Forest cannot therefore be considered to form a distinct stratum, so that the consociation has three stories only. There is: (i) a somewhat open but regularly spaced bottom story up to about 11 m. (35 ft.) high composed of small trees whose crowns are not usually in lateral contact and do not form a closed canopy. Above the bottom story there is: (ii) a reasonably regular middle layer of trees 11–21 m. (35–70 ft.) high, which fill the gaps between the stems of the top-story trees but which are rarely perfectly developed immediately below them. The crowns of these middle-story trees are usually elongated or oblong and are generally in lateral contact except (sometimes) beneath larger trees. The middle and bottom layers normally form together an almost closed (lower) canopy. Above them is: (iii) the top story, consisting of an irregular mass of trees 21 m. (70 ft.) high and upwards forming a closed (upper) canopy. The average level of the top of this story, in which very few species are represented, is about 36 m. (120 ft.), but emergent individuals reach considerably higher. In P.P. 4 there are only two species in the top story, the tallest specimen 41 m. (135 ft.) high. Of the ten middle-story trees in the plot only one is a young individual, nine trees of three species forming the layer. In the bottom story there are twenty-eight trees of eight species, of which four individuals of three species are immature.

*Swamp Forest*. No profile diagram was prepared for Swamp Forest. It is probably two-storied.

*Ecotones*. In areas of transition between Colonizing Forest and Mixed Forest it is usually impossible to distinguish any layering, at any rate in the midway stage. In ecotones between Mixed Forest and Ironwood Forest there are three ordinary stories and an emergent story. The chief emergent trees in the early stages of transition are mahoganies. Later, few emergent trees except *Cynometra* can be found.

*Characteristics of the strata*. In Budongo, as in other tropical rain forests, the trees of each stratum have characteristic features. *Top-story species* such as *Alstonia*, *Chrysophyllum* spp., *Cynometra*, *Entandrophragma* spp., *Khaya*, *Klainedoxa*, *Maesopsis*, *Mildbraediodendron*, *Olea*, etc., have spreading (often umbrella-shaped) crowns 'supported by a candelabra-like system of branches in which the main axis is rarely well marked above the first fork' (Richards, 1939). In Mixed Forest and Ironwood Forest the stems of these

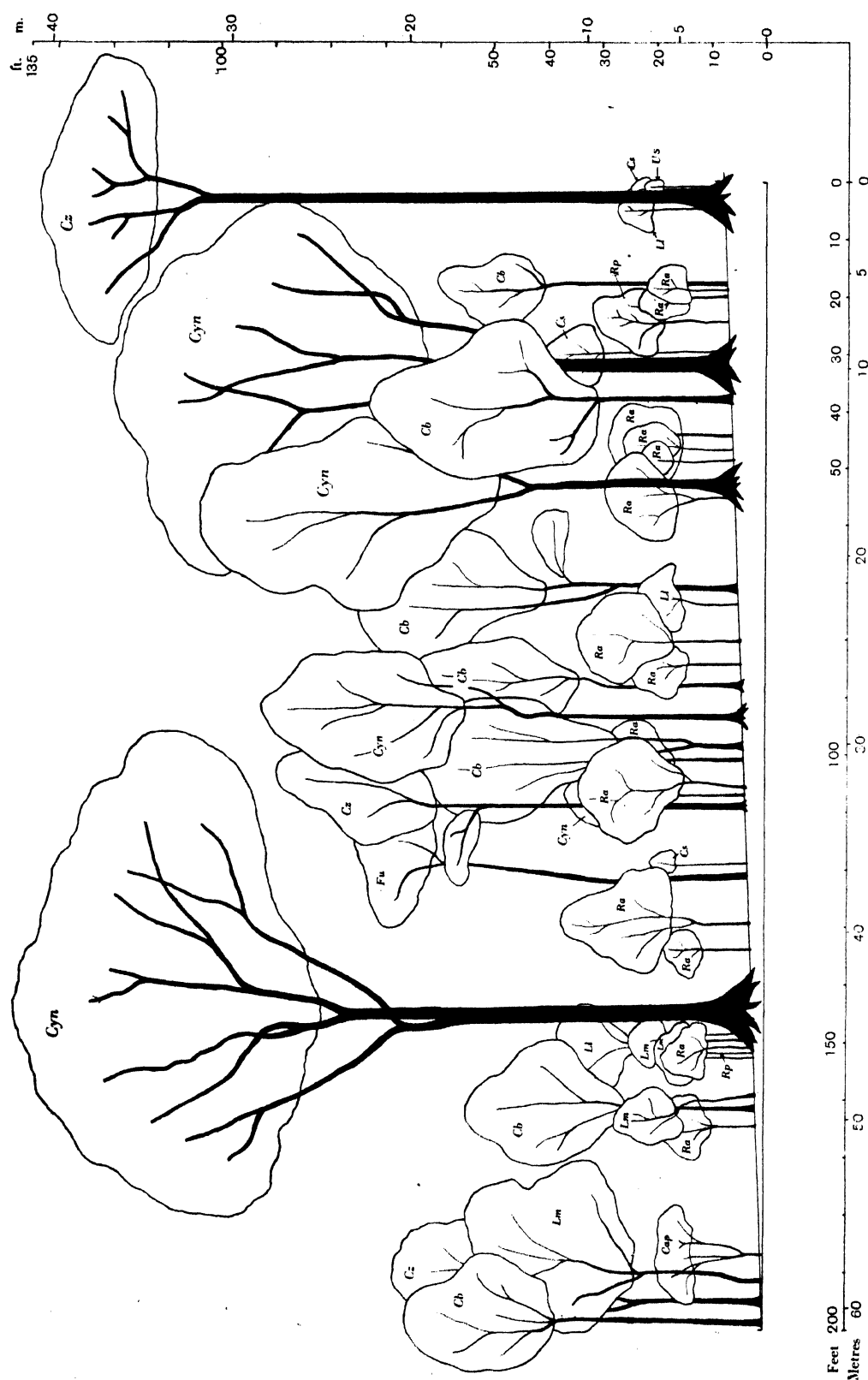


Fig. 9. Profile diagram of Ironwood Forest, Budongo. The diagram represents a strip of forest 61 m. (200 ft.) long and 7.6 m. (25 ft.) wide. The following are based on measurements and drawn strictly to scale: position, diameter at breast height, total height, height to first branch, lower limit and spread of crown. It has been necessary as a convention to draw the crowns compact and dense (very rarely the case). The plot contained forty-four trees 4.6 m. (15 ft.) high and over. All are shown.

top-story trees are usually either heavily buttressed or fluted. The leaves (or leaflets) are mostly small (sometimes very small, e.g. *Cynometra*) and have very short acumens (*Olea* is an exception). At Budongo nearly all the top-story trees are deciduous after a fashion, i.e. shed all their leaves at once but are leafless only for a few days and seldom all the trees of one species at the same time. *Maesopsis* is a noticeable exception, whole stands of this species remaining leafless for weeks on end in severe dry seasons. In the climax forest only a few ironwood are leafless at a time, so that the consociation as a whole is always reasonably densely foliated.

*Taller middle-story trees* such as *Bosqueia*, *Celtis soyauxii*, *Funtumia* spp., *Maba*, etc., have small conical evergreen crowns with the main axis of the stem distinct almost to the top of the tree\*. The leaves of these trees are usually rather small (*Funtumia* is an exception) and have slightly longer acumens than the leaves of top-story species. Buttresses are not usual; if present, they do not extend far up the stem.

*Shorter middle-story trees* (e.g. *Celtis brownii*) have larger, oblong, much-branched evergreen crowns. The leaves are broader and have longer acumens. The stems are unbuttressed. The only cauliflorous tree at Budongo, figs excepted, is a member in this layer. It is *Drypetes ugandensis* Hutch. (E. 3078).

*Bottom-story species* (e.g. *Rinorea ardisiaeflora*) are more variable. They tend to have rather small, pyramidal crowns and slender unbuttressed stems. Their leaves vary greatly in size from species to species, from small to (more usually) large. The acumen is usually long.

*Extreme height.* Although trees 61–64 m. (200–210 ft.) high occur at Budongo they are definitely rare. I have seen several *Entandrophragma cylindricum* of this order of height, and one specimen of *Bombax reflexum*. Accurate measurements of these trees, which are still standing, are not available. Among the mahoganies especially, heights of 50–55 m. (165–180 ft.) are frequent.

*Leaf size.* Most Budongo trees have leaves which correspond with the size limits of the lower half of Raunkiaer's mesophyll class. Only six of the commoner species do not have mesophyll leaves. They are *Cynometra alexandri* (nanophyll-microphyll); *Erythrophleum guineense*, *Phyllanthus discoideus* and *Rinorea ardisiaeflora* (microphyll); *Celtis soyauxii* and *Maesopsis eminii* (microphyll-mesophyll). The dominant species in Swamp Forest (*Mitragyna stipulosa*) has macrophyll leaves: the subdominant (*Pseudospondias microcarpa*) has mesophyll leaves.

Trees with macrophyll leaves are far from common. Only four species occur at all frequently, namely, *Cola cordifolia*, *Macaranga schweinfurthii*, *Mitragyna stipulosa* and *Myrianthus arboreus*. Two of these trees, *Macaranga* and *Mitragyna*, are confined to Swamp Forest. A third, *Myrianthus*, is commoner in Swamp Forest than elsewhere. Leptophyll species (e.g. *Piptadenia africana*) are even rarer than macrophyll. Nanophyll species are less uncommon. They are chiefly leguminous and include *Albizia*, *Cathormion*, *Parkia*, etc.

## (2) *Shrub and herb strata*

Beneath the lowest story of trees is a stratum of shrubs and beneath the shrubs is a stratum of herbs not normally exceeding 1 m. (3 ft.) in height. The shrub stratum merges imperceptibly with the lowest layer of trees and is not cut off sharply from it as might

\* Exceptional middle-story individuals which reach the top story tend to produce branched spreading crowns like those of normal constituents of that layer. An example is *Celtis soyauxii*.



appear from the profile diagrams where no plants less than 4.6 m. (15 ft.) high are shown.

The shrub stratum varies greatly in density, but except in the rattan cane thickets of Swamp Forest it is possible almost everywhere in Budongo to walk about or to push through the undergrowth without cutting a path, and to see some little distance ahead. Where old trees have fallen and gaps have resulted the undergrowth is always thicker. In Ironwood Forest the shrub layer is sparser than in the other forest types and the visibility is correspondingly longer (see descriptions of S.P.'s, pp. 43-5).

In Budongo, as in the rain forests of Nigeria, true shrubs are few both in species and individuals. Some of them (e.g. *Rinorea poggei*) 'have a fairly typical shrubby form, with no main axis', others (e.g. *Belonophora glomerata*) 'are remarkable for having a single main axis straight and branched only at the top, if at all: they resemble trees in miniature. The prevailing type of leaf is similar to that in the undergrowth tree stratum, entire or at most slightly serrate, with a long fine acumen' (Richards, 1939, p. 24).

'The herb stratum is even more unevenly developed than the shrub stratum. Large patches of the forest floor may be almost bare, elsewhere, especially in openings, it may be entirely concealed by the growth of herbs and small tree seedlings' (Richards, 1939, p. 24). Counts of the number of shoots of herbs, seedling woody plants and ferns in five quadrats 3 m.sq. (9.8 ft.sq.) scattered at random in S.P. 8 showed a variation of 162 to 522 shoots per quadrat with a mean of 335.

The density of the stratum is apparently dependent partly on shade, partly on root competition and partly on the depth, composition and structure of the top soil. Although a detailed study of the herb stratum of Budongo has yet to be made, its components are divisible, as in Nigeria, into (a) specialized shade-loving species, and (b) less specialized shade-tolerant species. As in Nigeria, also, such leaf features as drip-tips, velvet surfaces and metallic colourings are absent. Only three plants with variegated leaves are known to occur in Budongo, the undershrub *Acanthus montanus* T. Anders. (E. 2272), the ground orchid *Eulophidium liedevii* De Wild. (E. 5352), and a small rosette-forming herb not yet identified. A number of forest grasses are normal constituents of the stratum. The most important are *Leptaspis cochleata*, *Olyra latifolia*, *Oplismenus hirtellus* and *Streptogyne gerontogaea*. Bulbous-rooted herbs are not common. Ground orchids and aroids apart, the only bulbous-rooted species encountered at all often are *Haemanthus cinnabarinus* Decne. (E. 1998) and *Kaempferia macrosiphon* Baker (E. 1197). They occur both in Mixed Forest and Swamp Forest. *Selaginella versicolor* Spring (E. 2107) is the only species of *Selaginella* yet recorded from Budongo. It is very rare.

### (3) Climbers

The climbers of Budongo form three synusia: (a) a layer of lianas usually 20-24 m. (65-70 ft.) or more in height; (b) a layer of tall, strong (but not woody) climbers attaining about 9-15 m. (30-50 ft.), with exceptional taller individuals; and (c) a layer of small (mainly herbaceous) climbers which seldom reach higher than 7-9 m. (23-30 ft.). All three layers are not necessarily represented in any one type of forest.

The lianas of group (a) are absent from the early stages of Colonizing Forest, appearing only when development to Mixed Forest is well advanced. They are very abundant in Mixed Forest, where the synusia is at its maximum development, become less frequent as *Cynometra* increases in dominance, and are very scarce indeed in climax Ironwood Forest.

They are very abundant in Swamp Forest. Some Budongo lianas are cauliflorous, e.g. *Clerodendron kentrocaule* and *Tiliacora* spp.

The tall soft-stemmed climbers of group (b) are common in Colonizing Forest, and occasional in Mixed Forest and Ironwood Forest. Small climbers of group (c) are abundant in Colonizing Forest, occasional in Mixed Forest and absent or almost absent from the climax. The general position is brought out in the following table, in which the data from the S.P.'s are summarized. Numbers, where given, are approximate:

S.P.	Type of forest	Lianas	Tall climbers	Small climbers
1	Woodland Forest	None	14	Numerous
2	<i>Maesopsis</i> Forest	None	Frequent	Very numerous
3	<i>Maesopsis</i> Forest	24	Few	Numerous
4	Ecotone	38	Few	Few
5	Mixed Forest	73	Few	Occasional
6	Mixed Forest	70	Several <i>Culcasia</i>	None
7	Ecotone	27	None	None
8	Ecotone	31	One <i>Vanilla</i>	None
9	Ironwood Forest	9	None	None
10	Ironwood Forest	6	None	None
11	Swamp Forest	44	<i>Culcasia</i> very frequent; <i>Calamus</i> abundant	Few

It was found impossible to include climbers, even lianas only, in the profile diagrams. Had they been drawn, the lianas would be seen to spread from tree to tree, often binding the canopy so tightly together that to fell a selected tree several other trees must be cut as well.

Characteristic members of the three synusia are:

(a) Lianas: *Alafia schumannii* Stapf (E. 1562), *Clerodendron kentrocaule* Baker (E. 2207), *Clitandra orientalis* K. Schum. (E. 87), *Combretum* spp., *Dichapetalum ugandense* M. B. Moss (E. 3008), *Entada phaseoloides* Merr. (E.sn.), *Hippocratea* spp., *Landolphia dawei* Stapf (E.sn.), *L. florida* Stapf (E. 2343), *Pisonea aculeata* Linn. (E.sn.), *Securidaca welwitschii* Oliv. (E. 703), *Strychnos aculeata* Solered. (E. 3817), *Tiliacora* sp. (E. 2225), *Uncaria africana* G. Don (E. 3733).

(b) Tall climbers: *Buettneria africana* Mast. (E. 3835), *Calamus deerratus* Mann. & Wendl. (E. 1626) —woodier than the rest but scarcely a liana, *Canthium* spp., *Cissus* spp., *Culcasia scandens* Beauv. (E.sn.), *Ipomoea* spp., *Mussaenda* spp., *Piper guineense* Thonn. (E.sn.), *Popowia littoralis* Bagsh. & Bak. f. (E. 2003), *Rutidea* spp., *Sericostachys scandens* Gilg & Lopr. (E. 138), *Urera hypselodendron* Wedd. (E. 2115), *Vanilla imperialis* Kraenzl. (E. 2062).

(c) Small climbers: *Abrus* spp., *Afromendonia gilgiana* Lindau, *Artabotrys nitidus* Engl. (E. 431), *Clerodendron capitatum* Schum. & Thonn. (E.sn.), *Ipomoea* spp., *Rhynchosia* spp., *Tetracera potatoria* Afz. (E. 450), and many more.

#### (4) Epiphytes

Vascular epiphytes (flowering plants and ferns) are well represented. A general idea of the number of species on different kinds of tree, and of their abundance in various types of forest, was obtained from the data from the profile plots. In these plots the maximum number of species of epiphytes on a single tree is twenty-six but elsewhere in the forest I have collected between forty and forty-five species from an especially suitable 'host'. Excluding hemi-epiphytic figs, nearly one hundred species of vascular epiphytes have been collected from Budongo, embracing between twenty-five and thirty species of ferns,

about sixty species of orchids, and about ten species of other epiphytic plants. Epiphytes are more abundant in Budongo than in the Nigerian forests examined by Richards (where it was estimated that not more than thirty-five species occurred) and more abundant also than in the Cameroons (Engler, quoted by Richards, 1939, p. 27). Epiphytes are found on trees of every stratum but are much more frequent in the top story than in the understory. As in Nigeria, they 'occur chiefly on the largest individuals of each species of tree, which indicates that effective colonization by epiphytes only begins late in the life of the tree' (Richards, 1939, p. 30). This accounts, in part at least, for the scarcity of epiphytes in Colonizing Forest, although the lower humidity in this type is important also.

Another factor which influences the distribution of epiphytes is the nature of the bark of the host. As a rule only shaggy-barked species are heavily colonized, a good example being *Entandrophragma utile*, whose branches are nearly always smothered with epiphytes. Smooth-barked species, e.g. *Cynometra*, rarely carry epiphytes until they are so old that the branches have begun to die back, when they too may be fairly heavily colonized. Exceptional in their tastes are the two orchids *Ancistrochilus rothschildianus* O'Brien (E. 2277) and *Eulophiopsis lurida* Schltr. (E. 5183), which prefer to grow on the boles of smooth-barked trees.

Speaking generally, epiphytes are rare in Woodland Forest, commoner in *Maesopsis* Forest, and abundant in Mixed Forest. About the same number of species of epiphytes is found in Ironwood Forest as in Mixed Forest, but the number of individuals per unit of area is usually smaller. In Swamp Forest, epiphytes are common but the species encountered are often different from those of dry-land forest, many being very rare except in this type. *Angraecum infundibulare* Lindl. (E. 2040) is a good example. It is rare except near water.

The epiphytic flora of the four profile plots is summarized below. Epiphytic figs are not included:

P.P.	Type of forest	No. of trees in plot	% of trees colonized by epiphytes	No. of species of epiphytes			
				Ferns	Orchids	Other vascular epiphytes	Total
1	Woodland Forest	63	1.4	6	2	1	9
2	<i>Maesopsis</i> Forest	69	11.7	3	9	2	14
3	Mixed Forest	67	16.3	8	15	2	25
4	Ironwood Forest	44	22.7	7	24	4	35

*Hemi-epiphytes*. The only hemi-epiphytes are the strangling figs. At least ten species occur.

#### (5) *Parasites and saprophytes*

The root parasite *Thonningia ugandensis* Hemsl. (E. 1178) is the only true parasite recorded from Budongo. It is common both in Mixed Forest and Ironwood Forest. Hemi-parasites (epiphytic parasites) are represented by a few species of *Loranthus*, including *L. usuiensis* Oliv. (E. 2015) and *Loranthus* sp. (E. 2051).

The only saprophytic flowering plant known to occur in the forest is the tiny *Afrothismia winkleri* Schltr. (E. 4041). Three specimens were growing amongst damp dead leaves on a flattened termite mound in S.P. 5.

## VI. SUMMARIZED DESCRIPTIONS OF THE FOREST TYPES

(1) *Colonizing Forest*

Colonizing Forest is two-storied. It is characterized by its low height-growth (trees exceeding 33 m. (110 ft.) in height are rare), by the lack of trees of large diameter, by the scarcity of buttresses, and by the absence of lianas. Nearly all the top-story trees are deciduous in the hot weather, shedding their leaves at about the same time. The duration of leaflessness (usually a matter of weeks) depends in part at least on the severity of the dry season. Because the lower story, too, is composed chiefly of deciduous species, the undergrowth layers become much desiccated in the hot weather, shrubs wilting, many herbs dying, and the ground becoming dry and cracked. Due partly to the low humidity and partly to the scarcity of suitable mature hosts, vascular epiphytes are few in number and in species. Mosses and lichens are scarce, creepers and soft-stemmed climbers abundant. The presence of abandoned termite mounds of a grassland type is a constant feature, often associated with denser patches of growth. The younger stages of Colonizing Forest are characterized by the presence of relic grassland species, noticeably *Terminalia velutina*. In the more advanced stages there is an increasing admixture of Mixed Forest trees.

*Woodland Forest.* The Woodland associates of Colonizing Forest occurs on poor or shallow soils. It is found, for example, on the sides of ridges whose flatter and more fertile tops carry *Maesopsis* Forest. In Woodland Forest the top story is composed of a mixture of species forming a very uneven broken canopy. Small almost pure patches of *Olea welwitschii* sometimes occur. *Caloncoba schweinfurthii* is nearly always dominant in the understory.

In S.P. 1, *Olea welwitschii*, *Phyllanthus discoideus* and *Sapium ellipticum* are co-dominant in the top story, forming 52% of the trees 41 cm. (16 in.) d.b.h. and over. *Terminalia velutina* accounts for a further 20% of the trees of this class, but most of the individuals are dying. *Caloncoba schweinfurthii* forms 31% of the understory trees 10–40 cm. (4–16 in.) d.b.h.

*Maesopsis Forest.* The *Maesopsis* consociates of Colonizing Forest is found on deeper and better soil than Woodland Forest. The top story is strikingly even, having the appearance of an eiderdown quilt when viewed from above (Pl. 2, phot. 3). *M. eminii* is the canopy dominant, forming 50–80% of trees 41 cm. (16 in.) d.b.h. and over (58% in S.P. 2; 70% in S.P. 3). *Caloncoba schweinfurthii* is usually dominant in the understory except where development to Mixed Forest is well advanced, when *Celtis brownii* and/or *Maba abyssinica* may be codominant or dominant.

In S.P. 2, *Olea welwitschii* is subdominant in the canopy, forming 20% of all trees 41 cm. (16 in.) d.b.h. and over. *Caloncoba schweinfurthii* is dominant in the understory, forming 52% of stems 10–40 cm. (4–16 in.) d.b.h.

In S.P. 3, the canopy subdominant is *Phyllanthus discoideus* (11%). *Celtis brownii* and *Maba abyssinica* are codominant in the understory, accounting for 40% of the smaller trees (18 and 22% respectively).

(2) *Mixed Forest*

It is stated by Davis & Richards (1934) that single-species dominance is exceptional among rain-forest communities. If this is so, then (Woodland Forest apart) Mixed Forest is the only forest type in our area which approaches normality. Even here, as in the

Mixed Forest association of British Guiana (Davis & Richards, 1934), a small number of closely allied species are together clearly dominant.

The Mixed Forest associates covers most of Budongo. It is recognizable by its four tree layers, by the diversity of its species, by the great height of the canopy (the main story averages 21–36 m. (70–120 ft.), with emergent trees 36–55 m. (120–180 ft.) or more), by the abundance of trees of large diameter (with stems usually either provided with large thick buttresses or deeply fluted like the folds of a curtain), and by the abundance of vascular epiphytes and lianas. 'Owing to the large number of species, none of which is abundant enough to lend the associates as a whole a special appearance, it has the varied aspect usually considered characteristic of tropical forest' (Davis & Richards, 1934, p. 117).

The trees of the emergent story of Mixed Forest are nearly all deciduous, but shed their leaves for a short period only and not all the trees, even of a single species, together. In the main layer there is always a fair admixture of evergreen species and of *Cynometra alexandri* (leafless for a few days only), so that the upper canopy as a whole is never totally leafless or anything approaching that state. For this reason, and because the lower strata are almost entirely evergreen, there is less desiccation of the undergrowth layers and of the surface soil than in any other forest type at Budongo except Swamp Forest. Relic termite mounds of grassland origin are still discernible although often difficult to pick out.

In the two Mixed Forest S.P.'s the most abundant large trees are:

Species	% of all trees 41 cm. (16 in.) diam. and over	
	S.P. 5	S.P. 6
<i>Alstonia congensis</i> Engl.	10.1	9.9
<i>Chrysophyllum albidum</i> G. Don	6.3	9.9
<i>Chrysophyllum perpulchrum</i> Mildbr. ex Hutch. & J. M. Dalz.	5.1	3.0
<i>Chrysophyllum</i> n.sp.? (E. 2248)	11.4	11.9
<i>Cynometra alexandri</i> C. H. Wright	2.5	23.8
<i>Khaya anthotheca</i> C.DC.	2.5	15.8
<i>Trichilia prieuriana</i> A. Juss.	10.1	1.0
7 species	48.0	75.3

Although there is no single dominant in S.P. 5 the three timber-producing species of *Chrysophyllum* taken together form 23% of the canopy trees, and are together clearly dominant. *Alstonia congensis* and *Trichilia prieuriana* are the canopy subdominants.

In S.P. 6, the same three species of *Chrysophyllum* form 25% of the canopy and are together codominant with *Cynometra alexandri* (24%). *Alstonia congensis* and *Khaya anthotheca* are the canopy subdominants. The high percentage of *Cynometra* in S.P. 6 shows that development of Mixed Forest to Ironwood Forest is well advanced, so far advanced indeed that the plot is assuming the nature of an ecotone between the two types. Abundance of *Celtis soyauxii*, a small-crowned tree with a stem seldom more than 30 cm. (12 in.) d.b.h., is a constant feature of Mixed Forest. Although it attains its maximum abundance in this type, *C. soyauxii* is common also in the ironwood climax. In S.P.'s 5 and 6 all age classes of the tree are well represented and in both plots it is the dominant species 10–40 cm. (4–16 in.) d.b.h.

Between forty-three and fifty different species of canopy trees occur in Mixed Forest, a far larger number than in any other type.\*

\* Table 8 shows more species present in Swamp Forest (S.P. 11) than in Mixed Forest. The reason is that the swamp plot contained patches of dry land, resulting in the inclusion of Mixed Forest species as well as those characteristic of Swamp Forest proper.

In S.P. 5 the number of species 41 cm. (16 in.) d.b.h. and over is twenty-seven; in S.P. 6 it is twenty-two.

The number of trees on a given area of Mixed Forest is higher than that on a similar area of Ironwood Forest. S.P.'s 5 and 6 (Mixed Forest) contain an average of 684 trees exceeding 10 cm. (4 in.) d.b.h. In S.P.'s 9 and 10 (Ironwood Forest) the corresponding figure is 570.

(3) *Ironwood Forest (climatic climax)*

The Ironwood Forest consociation has a characteristic appearance. *Cynometra alexandri*, the prevailing tree, is unmistakable. It has smooth grey-brown bark; very large thin plank buttresses; a relatively short, often very gnarled, bole; a huge tall spreading crown; and very small leaflets. In this type of forest, ironwood is overwhelmingly dominant, accounting for 20–35% of all trees present (21% in S.P. 9; 33% in S.P. 10); and for 75–90% of the trees 41 cm. (16 in.) d.b.h. and over (76% in S.P. 9; 85% in S.P. 10). No other canopy species is sufficiently abundant to be regarded as subdominant. In the two ironwood S.P.'s the nearest competitors to *Cynometra* are (in S.P. 9) *Strychnos* sp. (E. 1253), *Celtis soyauxii*, and *C. zenkeri* (9, 7 and 7% respectively); and (in S.P. 10) *C. zenkeri* (4%).

As a rule, *Lasiodiscus mildbraedii* is the dominant understory tree in Ironwood Forest, cf. S.P. 9, where it forms 62% of all trees 10–40 cm. (4–16 in.) d.b.h. Occasionally *Lasiodiscus* may be entirely lacking, e.g. S.P. 10, where it is replaced by *Lepidoturus laxiflorus* (29%).

A feature of the ironwood climax is the small number of species which occur. In S.P. 9 only eleven species, and in S.P. 10 only twenty-five species, exceed 10 cm. (4 in.) d.b.h., as compared with fifty-eight and fifty-three species in the Mixed Forest S.P. 5 and 6 respectively. Although the consociation is comparatively well illuminated, the shrub and small tree layers are poorly developed. A possible explanation is that *Cynometra* is a 'greedy feeder', so greedy, indeed, that where it is present in quantity it not only reacts unfavourably on other species but also limits its own development. This may be the reason why the purer the stand of ironwood, the smaller the individual trees, and why the largest specimens of *Cynometra* are found not in Ironwood Forest but in Mixed Forest and in its ecotones with the climax. This fact, visually obvious in the field, was confirmed by measurements made in S.P.'s 8 and 10. In both plots 71% of the *Cynometra* exceed 41 cm. (16 in.) d.b.h. In S.P. 8 (ecotone) 15% of these larger trees exceed 150 cm. (60 in.) diam. above buttress; in S.P. 10 (Ironwood Forest) only 4% attain this size.

Partly because of the poor development of the shrub layer, which affords little protection to smaller plants, and partly because of the powdery nature of the upper layers of the soil, the herb stratum in *Cynometra* forest becomes parched in the dry season. The stand then presents a very wilted appearance, far removed from the general conception of rain forest and suggesting a much drier type. Even in the rains there is little tropical lushness, the non-tropical appearance being accentuated by the lack of lianas and by the long visibility.

Ironwood forest shows excellent stocking of *Cynometra* of all sizes, from saplings upwards, as shown in Table 7.

Plants smaller than saplings are far from abundant but are sufficient to replace any casualties which occur in understory and canopy. Seedling mortality is colossal. Towards the end of the rainy season it is difficult to walk anywhere within the consociation without trampling on *Cynometra* seedlings. Four to five months later, at the end of the dry season,

careful search is needed to find any young plants at all. A low seedling survival rate of canopy trees is a feature of rain forest not only in Uganda but in Africa as a whole (see Richards, 1939, p. 19).

Table 7. *Distribution of diameter classes, Ironwood Forest, S.P.'s 9 and 10*

	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	Over 60 cm. (over 23 in.)
S.P. 9: No. of <i>Cynometra</i>	21	13	7	6	6	71
% of all trees	5.5	15.7	38.9	54.5	60.0	80.7
S.P. 10: No. of <i>Cynometra</i>	5	18	10	14	7	61
% of all trees	2.6	40.9	52.6	73.7	77.8	88.4

#### (4) *Swamp Forest (edaphic climax)*

Swamp Forest is a 'type of high forest which is flooded in the wet season and water-logged to within a few centimetres of the soil surface during the rest of the year. Where it abuts on gently rising ground a gradual transition from it to Mixed Rain Forest may be seen, but it does not appear to show any appreciable tendency to develop into this or any other type of vegetation. . . . It is doubtful if it ever would do so without a change in the water level due to some external cause and it is therefore regarded as an edaphic climax' (Richards, 1939, p. 42). The above remarks concerning the Swamp Forest of Nigeria apply equally to Swamp Forest in Uganda. At Budongo, this type of forest does not cover large areas but is confined to narrow strips of low-lying land in valley bottoms, the strips seldom more than 90 m. (300 ft.) wide. The single sample plot (S.P. 11) enumerated in this type is not entirely satisfactory. It contained some quite typical Swamp Forest but was by no means level throughout, the raised (drier) ground carrying patches of Mixed Forest with a high admixture of *Cynometra*. Data from the plot must therefore be treated with reserve.

In the absence of profile data it is impossible to be certain of the stratification, but as far as can be judged Swamp Forest is two-storied. The canopy is much more irregular and broken than that of Mixed Forest, tangles of small trees and bushes alternating with patches where the large trees are smothered with rattan (*Calamus*). Other patches consist of almost pure stands of *Mitragyna* distributed regularly throughout a breast-high undergrowth composed mainly of *Marantochloa*. A noticeable feature is the abundance of lianas and of strangling figs. Double-stemmed trees are frequent.

Of the eighty tree species in S.P. 11, fifteen are almost entirely confined to swamp or riparian forest and are found only exceptionally on dry ground sites. These fifteen species are: *Bombax reflexum* Sprague, *Cathormion altissimum* Hutch. & Dandy, *Cleistanthus* sp. probably *C. polystachyus* Hook. f. ex Planch. (E. 3081), *Cleistopholis patens* Engl. & Diels, *Erythrina excelsa* Baker, *Euphorbia teke* Schweinf. ex Pax, *Macaranga schweinfurthii* Pax, *Mitragyna stipulosa* O. Ktze., *Parkia filicoidea* Welw., *Phoenix reclinata* Jacq., *Pseudospondias microcarpa* Engl., *Spondianthus ugandensis* Hutch., *Treculia africana* Decne., *Tylostemon ugandensis* Stapf, and *Voacanga obtusa* K. Schum. Only one of these species, *Pseudospondias microcarpa*, is heavily buttressed, so that there is even less buttressing in the Swamp Forest of Budongo than in that of Nigeria (see Richards, 1939, p. 45).

Notwithstanding the fact that the plot contained a certain amount of dry-ground forest, the most abundant tree in S.P. 11 is the swamp-loving *Mitragyna stipulosa*. It is dominant both in understory and canopy, forming 17% of trees 10 cm. (4 in.) d.b.h. and over, and

21 % of trees 41 cm. (16 in.) d.b.h. and over. *Pseudospondias microcarpa* is subdominant in the canopy. This *Mitragyna-Pseudospondias* mixture is typical of Swamp Forest throughout Uganda, associated understory species usually including *Neoboutonia* spp. and *Voacanga obtusa*. The percentage of *Mitragyna* present is often (probably usually) much higher than in S.P. 11. In Buganda, especially, this tree commonly forms 'verticillate plantations' on the edge of papyrus swamps (cf. Richards, 1939, p. 47).

A feature of Swamp Forest for which I can suggest no satisfactory explanation is the unusual frequency of trees with armed stems, a character which is often apparent only on young individuals, disappearing as the trees grow old. The spines vary from sharp, hard and elongated, e.g. *Dichrostachys*, to blunt, corky, soft and conical, e.g. *Bombax*. Of the eighty different trees recorded from S.P. 11, no fewer than nine species were armed: *Bombax reflexum*, *Bridelia micrantha* (young), *Chaetacme microcarpa*, *Dichrostachys glomerata*, *Erythrina excelsa*, *Fagara angolensis*, *Fagaropsis angolensis* (one young plant only), *Klainedoxa gabonensis* (young), and *Macaranga schweinfurthii* (young). Several Swamp Forest climbers, too, are armed, e.g. *Calamus*.

Apart from the shrubby *Dracaena fragrans* Ker-Gawl. (E. 1423), which is extremely rare, no plants of special life-forms (palms, rattans, bamboos, etc.) are found in dry land forest at Budongo. In Swamp Forest, on the other hand, the following occur: *Dracaena laxissima* Engl. (E. 3744) (Agavaceae, sub-scandent bush, frequent to abundant), *Oreobamboos buchwaldii* K. Schum. (bamboo, locally gregarious, nowhere common), *Euphorbia teke* Schweinf. ex Pax. (*Candelabra euphorbia*, common), *Phoenix reclinata* Jacq. (palm, common on some Swamp Forest margins), *Raphia monbuttorum* Drude. (palm, extremely rare), *Calamus deerratus* Mann. & Wendl. (rattan cane, very abundant), *Pandanus chiliocarpus* Stapf (screw pine, rare, confined to a few stream-beds).

## VII. COMPARISONS

### (1) Comparison of forest types

*Density of stocking.* The number of trees per unit of area varies considerably from place to place within the same type of forest (Table 8). Even so, it is clear from the S.P. data that as grassland develops through Colonizing Forest to Mixed Forest there is a steady rise in the number of woody stems per unit of area, reaching a maximum figure of about 480 trees per hectare (= 195 per acre) in the later stages of transition from Colonizing Forest to Mixed Forest, and in Mixed Forest proper. Thereafter, coinciding with the increasing dominance of *Cynometra*, there is a marked decline in total stocking till finally in climax Ironwood Forest there are actually fewer trees per unit of area (about 316 per hectare = 128 per acre) than in Colonizing Forest only 30–40 years old (about 345 stems per hectare = 140 per acre).

Although there is a higher total stocking of trees in Mixed Forest than in either Colonizing or Ironwood Forest, this is not true of trees 41 cm. (16 in.) d.b.h. and over, which are most abundant (in dry-land forest) in the *Maesopsis* consociates of Colonizing Forest (S.P. 3), and in Ironwood Forest (S.P. 9 and 10), i.e. in the two types of dry land forest which exhibit clear single-species dominance. In both these types there are about 70 trees per hectare (= 28 per acre) exceeding 41 cm. (16 in.) d.b.h., a frequency much greater than the figure of 56 per hectare (= 23 per acre) in Mixed Forest and its ecotones (S.P. 4–8).

The Swamp Forest S.P. is the only one of the eleven S.P.'s enumerated at Budongo in



Table 8. Comparison of sample plots

	Colonizing (Woodland) Forest			Colonizing ( <i>Maesopsis</i> ) Forest			Ecotone	Mixed Forest		Ecotone		Ironwood Forest		Swamp Forest S.P. 11
	S.P. 1	S.P. 2	S.P. 3	S.P. 2	S.P. 3	S.P. 4		S.P. 5	S.P. 6	S.P. 7	S.P. 8	S.P. 9	S.P. 10	
No. of trees 10 cm. (4 in.) diam. and over	473	556	762	556	762	778		752	617	699	548	593	349	562
Do. per hectare	317	373	511	373	511	523		504	414	469	368	398	234	377
Do. per acre	129	151	208	151	208	212		205	168	190	149	162	95	153
No. of trees 20 cm. (8 in.) diam. and over	199	308	281	308	281	298		336	280	215	280	210	160	275
Do. per hectare	141	217	198	217	198	210		237	183	151	197	148	113	194
Do. per acre	57	88	80	88	80	85		96	74	61	80	60	46	79
No. of trees 41 cm. (16 in.) diam. and over	60	59	105	59	105	87		79	101	69	83	109	97	124
Do. per hectare	40	39	70	39	70	58		53	68	46	56	73	65	83
Do. per acre	16	16	29	16	29	24		21	27	19	23	30	26	34
No. of species 10 cm. (4 in.) diam. and over	35	34	38	34	38	58		58	53	49	31	11	25	80
No. of species 20 cm. (8 in.) diam. and over	25	21	29	21	29	43		41	38	36	28	10	18	57
No. of species 41 cm. (16 in.) diam. and over	16	8	12	8	12	23		27	22	15	15	6	13	33
Most abundant species 10 cm. (4 in.) diam. and over	<i>Caloncoba schweinfurthii</i> Gilg	<i>Caloncoba schweinfurthii</i> Gilg	<i>Maba abyssinica</i> Hiern	<i>Caloncoba schweinfurthii</i> Gilg	<i>Maba abyssinica</i> Hiern	<i>Trichilia hudebottii</i> Planch.		<i>Celtis soyauxii</i> Engl.	<i>Celtis soyauxii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Cynometra alexandri</i> C. H. Wright	<i>Mitragyna stipulosa</i> O. Ktze.
Percentage	28	46	19	46	19	23		32	35	26	39	53	33	17
Most abundant species 20 cm. (8 in.) diam. and over	<i>Caloncoba schweinfurthii</i> Gilg	<i>Caloncoba schweinfurthii</i> Gilg	<i>Maesopsis emini</i> Engl.	<i>Caloncoba schweinfurthii</i> Gilg	<i>Maesopsis emini</i> Engl.	<i>Funtumia latifolia</i> Stapf ex Schltr.		<i>Celtis soyauxii</i> Engl.	<i>Celtis soyauxii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Cynometra alexandri</i> C. H. Wright	<i>Cynometra alexandri</i> C. H. Wright	<i>Mitragyna stipulosa</i> O. Ktze.
Percentage	30	32	30	32	30	39		21	20	27	34	58	69	25
Most abundant species 10-40 cm. (4-16 in.) diam. and over	<i>Caloncoba schweinfurthii</i> Gilg	<i>Caloncoba schweinfurthii</i> Gilg	<i>Maba abyssinica</i> Hiern	<i>Caloncoba schweinfurthii</i> Gilg	<i>Maba abyssinica</i> Hiern	<i>Trichilia hudebottii</i> Planch.		<i>Celtis soyauxii</i> Engl.	<i>Celtis soyauxii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Lasiodiscus mildbraedii</i> Engl.	<i>Lepidoborus lariflorus</i> Benth.	<i>Mitragyna stipulosa</i> O. Ktze.
Percentage	31	52	22	52	22	26		35	42	37	46	62	29	15
Most abundant species 41 cm. (16 in.) diam. and over	<i>Olea welwitschii</i> Gilg & Schellenb.	<i>Maesopsis emini</i> Engl.	<i>Maesopsis emini</i> Engl.	<i>Maesopsis emini</i> Engl.	<i>Maesopsis emini</i> Engl.	<i>Maesopsis emini</i> Engl.		<i>Chrysophyllum</i> 3 spp. together	<i>Chrysophyllum</i> 3 spp. together	<i>Cynometra alexandri</i> C. H. Wright	<i>Cynometra alexandri</i> C. H. Wright	<i>Cynometra alexandri</i> C. H. Wright	<i>Cynometra alexandri</i> C. H. Wright	<i>Mitragyna stipulosa</i> O. Ktze.
Percentage	22	58	70	58	70	31		23	25	43	64	76	85	21

which the same tree is dominant in all diameter classes both of overwood and underwood. Although, as has been stated, the figures from this plot must be treated with reserve, it fits well with the general picture that in Swamp Forest, where single species dominance is even more marked than in *Maesopsis* Forest and Ironwood Forest, the number of large trees per unit of area is higher than in any other type, amounting (on S.P. 11) to 83 per hectare (= 34 per acre).

*Number of species.* Just as the number of trees per unit of area varies not only from one forest type to the next but also from place to place within a single type, so too with the number of species. The variations within a single type can be judged from Table 8; those between different types from a comparison of mean S.P. figures:\*

Diameter class	Mean no. of species on plot of 1.418 ha. (= 3.673 acres)		
	Colonizing Forest (S.P. 1-3)	Mixed Forest (S.P. 5, 6)	Ironwood Forest (S.P. 9, 10)
10 cm. (4 in.) diam. and over	36	55	18
20 cm. (8 in.) diam. and over	25	39	14
41 cm. (16 in.) diam. and over	12	24	9

It is clear from these figures that there is a rise in the number of species as Mixed Forest develops from Colonizing Forest, followed by a fall in numbers as Mixed Forest is succeeded by Ironwood Forest. This is true not only of the total number of species present but also of canopy and understory species, taken separately.

From Table 8 it can be seen that a high degree of canopy dominance is directly associated with a low number of canopy species. There is little relation, if any, between the degree of canopy dominance and the number of species of all sizes which are present.

*Local variations in composition.* There is considerable variation in the numbers (and species) of trees occurring in different parts of the same type of forest. In other words, the associates, consocieties and consociations which contribute to the make-up of the forest are each composed of a number of locies and lociations† which differ in the subdominants and understory species present, and in the proportions in which these species occur. A good example of a lociation is found in Ironwood Forest. Here, as is indicated by the data from S.P. 7-9 and as has been confirmed by observations over the consociation as a whole, the normal understory dominant is *Lasiodiscus mildbraedii*. In certain parts of the consociation, however, this species is very scarce, and over small areas (as in S.P. 10) it may be entirely lacking—a well-marked lociation resulting. The factors which govern the formation of locies and lociations, and their relationships one with another, are imperfectly understood. Further work is needed to determine their exact standing.

*Buttressing.* In Colonizing Forest there is an almost complete absence of buttressed stems. In Mixed Forest buttressing is much commoner, many of the canopy species (e.g. *Entandrophragma angolense*, *E. cylindricum*, *Khaya anthotheca*, *Ficus mucoso*, *Khaya anthotheca*) having large thick buttresses which extend far up the trunk (Pl. 3, phot. 6). The amount of buttressing varies greatly from individual to individual within a single species. In the case of the mahoganies, the buttresses rarely become prominent till middle age. Certain Mixed Forest species, although attaining large size, have practically no buttresses. An example is *Mildbraediodendron excelsum*. Fluted stems are common, e.g. *Alstonia congensis*, *Trichilia prieuriana*.

\* Swamp Forest omitted.

† Terms used in the sense conceived by Carpenter (1936).

It is in Ironwood Forest that buttressing is best developed. Here the only common large tree without buttresses or flutings is *Strychnos* sp. (E. 1253). The enormous plank buttresses of *Cynometra*, extending many metres up the stem and far out from its base, are one of the most noticeable features of the type. Practically every individual is buttressed, usually very strongly, the buttresses appearing very early in life (Pl. 3, phot. 7). Of less abundant species, both *Celtis soyauxii* and *C. zenkeri* are buttressed, the latter strongly.

It is now generally accepted that the production of buttresses is related to edaphic factors, and that their development depends primarily on the absence of a taproot. All that part of Budongo which is now occupied by Ironwood Forest originally bore Mixed Forest, a type in which many of the trees are deep-rooted. It may be assumed, therefore, that *Cynometra alexandri* is a species which originally developed its buttressed nature in a shallow-soiled habitat, and that it has retained this hereditary character in the deeper soils of Budongo.

The dominant tree in Swamp Forest (*Mitragyna*) is always unbuttressed. The sub-dominant (*Pseudospondias*) is always heavily buttressed.

#### *Seasonal periodicity*

(a) *Flowering periodicity* has not been studied in detail so that only a few general observations can be given. In Ironwood Forest very few species are in flower in the period between the two rainy seasons and in the first part of the short rains. Towards the end of these rains the undershrub layer comes into flower and for almost two months the long white spikes of *Whitfieldia elongata* are everywhere conspicuous. A number of other Acanthaceae flower at the same time, but the dominant herb, *Lankesteria elegans*, does not bloom till the *Whitfieldia* is fading, its bright orange flowers brightening the undergrowth till the very end of the dry weather. In February, while *Lankesteria* is still in flower, the understory trees begin to blossom. One of the first is *Lasiodiscus mildbraedii*, followed soon afterwards by *Rinorea ardisiaeflora*, whose flowers open as the rains begin. With the coming of the wet season the majority of the large trees burst into flower and the canopy is soon white with the massed clusters of *Cynometra*.

In Mixed Forest and Colonizing Forest flowering succession is not so marked, but a well-defined seasonal rhythm is still apparent. As in Ironwood Forest, the main flowering of the canopy takes place at the start of the rains. In the case of the mahoganies, and many other species, the fruits take about nine months to mature, the seeds falling in the middle of the next dry season.

(b) *Leaf fall*. Truly deciduous species (bare for more or less long periods) are abundant only in Colonizing Forest, although a certain number, e.g. *Albizzia* spp., *Mildbraediendron excelsum*, etc., are found in Mixed Forest also. The period of leaflessness occurs at the end of the rainy season (November–December), or during the dry weather, but the trees flush before the rains break. Most Mixed Forest and Ironwood Forest species are neither truly evergreen nor truly deciduous. They lose all their leaves at once but produce new foliage almost immediately. Typical of this are *Cynometra*, *Entandrophragma* spp. and *Khaya*. The mahoganies tend to shed their leaves at the height of the dry weather; the ironwood at its start, or before the rains have finished.

Evergreen species are relatively rare in the canopy but are abundant in the lower stories, both in Mixed and Ironwood Forest.

(2) *Comparison with other Uganda forests*

Single-species dominance, as exhibited by the two climax types at Budongo, is a characteristic of almost all primary lowland rain forest in Uganda. Seven major forest blocks (Budongo, Bugoma, Kalinzu, Kibale with Itwara, Malabigambo, Semliki, and Zoka), belonging to the Lowland Rain Forest Subformation are found in the Western Province, which is the part of the Protectorate with which I am best acquainted. Six of these forests exhibit single-species dominance in the climax type, and in four of the six the climax is Ironwood Forest. The composition of the ironwood stands is essentially similar in all four forests, and Budongo is the only one of the four in which Ironwood Forest does not cover the greater part of the area (i.e. the only one in which there is a high percentage of Mixed Forest). Budongo, therefore, is probably younger than the rest.

Of the three other large blocks of Lowland Rain Forest in the Province, two lie just above the altitudinal limit of *Cynometra*, which is not found above 1400 m. (=4600 ft.) elevation. In both these forests *Cynometra* is replaced as climax dominant by the so-called grey plum—*Parinari excelsa* Sabine. One of the two forests, Kalinzu, is almost completely covered by the grey plum consociation; in the second, Kibale, a considerable part of the forest bears a Mixed Forest growth. As far as can be judged from casual inspection, this Mixed Forest of Kibale bears the same relation to Grey Plum Forest as does Mixed Forest to Ironwood Forest at Budongo.

The seventh Lowland Rain Forest to be considered is the Zoka forest in East Madi. This differs from the preceding six in consisting almost entirely of Mixed Forest of a type very similar to that of Budongo, but containing a greater proportion of mahogany (chiefly *Khaya grandifoliola* C.DC.). Here and there within the Zoka are small patches dominated by immature *Strychnos* sp. (E. 1253). This tree occurs sparingly in a number of other Uganda forests and at Budongo is the only large tree to compete successfully with *Cynometra* (cf. S.P. 9, where it is subdominant). Although there can as yet be no certainty in the matter, it is perhaps legitimate to assume that the small patches of *Strychnos* already present in the Zoka mark the start of invasion of Mixed Forest by *Strychnos* Forest, i.e. that in the Zoka forest, too, the climatic climax is a consociation.

(3) *Comparison with other regions*

Recent ecological studies of Primary Rain Forest (Davis & Richards, 1933-4; Vaughan & Wiehe, 1937 and 1941; Richards, 1936; Richards, 1939) have shown that in Mauritius, Sarawak and Southern Nigeria the climatic climax in the areas investigated is Mixed Forest. In British Guiana the primary forest (Moraballi Creek) consists of five distinct climax communities, four of them consociations. The fifth community which, because it occupies what is probably the optimum habitat, is believed to be the climatic climax, is again Mixed Forest. In Uganda, in contrast, the climatic climax is always, or nearly always, a consociation.

If the ironwood consociation of Budongo is compared with the mixed forest associations described from the above four regions (see Vaughan & Wiehe, 1941, p. 153), it is clear that apart from a rather vague similarity in general structure, they have few features in common.

If, on the other hand, the ironwood consociation of Budongo is compared (Table 9) with the four consociations described by Davis & Richards from British Guiana, very considerable

similarity is apparent. The only great difference, indeed, is in the number of species in the understorey. In the richer of the ironwood plots at Budongo (S.P. 10) there are only twenty-five tree species exceeding 10 cm. (4 in.) d.b.h.; and only eighteen exceeding 20 cm. (8 in.) d.b.h. In the poorest of the Guiana plots (Mora consociation) the corresponding figures are sixty and thirty-eight respectively. It is possible, though by no means certain, that the poverty of understorey species at Budongo is directly due to the ultra-dominance of *Cynometra*. The mean degree of dominance of this species both among trees 20 cm. (8 in.) d.b.h. and over (59%), and among trees 41 cm. (16 in.) d.b.h. and over (80%), is much greater than the degree of dominance exhibited by the most abundant species in any of the Guiana types, where the corresponding figures (Mora) are 32 and 67% respectively.

Table 9. Comparison of consociations, British Guiana and Uganda\*

	British Guiana (Moraballi Creek)				Uganda (Budongo)
	Mora Fine silt	Morabukea Heavy silt	Greenheart Sand	Wallaba Light sand	Ironwood†
Soil (lower sample) ...	<i>Mora excelsa</i>	<i>Mora gong-</i> <i>gripii</i>	<i>Ocotea</i>	<i>Eperua</i>	Tropical red earth
Dominant species ...	Benth.	(Kleinh.)	<i>rodioei</i> (Schomb.)	<i>falcata</i> Aubl.	<i>Cynometra</i> <i>alexandri</i> C. H. Wright
Dominance:					
As % of trees over 10 cm. (4 in.) diam.	23	27	9	21	27 (21, 33)
As % of trees over 20 cm. (8 in.) diam.	32	24	19	32	59 (49, 69)
As % of trees over 41 cm. (16 in.) diam.	67	61	43	67	80 (76, 84)
Number of individuals per hectare (=2.471 acres):					
10 cm. (4 in.) diam. and over	310	309	519	617	316 (398, 234)
20 cm. (8 in.) diam. and over	181	168	265	325	131 (148, 113)
41 cm. (16 in.) diam. and over	45	60	87	67	69 (73, 65)
Number of species on plot of 1.418 ha. (=3.673 acres):					
10 cm. (4 in.) diam. and over	60	71	91	95	18 (11, 25)
20 cm. (8 in.) diam. and over	38	46	65	46	14 (10, 18)
41 cm. (16 in.) diam. and over	11	21	33	15	10 (6, 13)
Percentage Leguminosae (individuals)	59	33	14	53	28 (22, 33)
Buttressing of dominant	Very strong	Strong	Very slight	None	Very strong
Abundance of strongly buttressed subsidiary species	Abundant	Frequent	Scarce	Rare	Frequent

\* Guiana data from Davis & Richards (1933-4).

† Mean figures, S.P. 9 and 10; figures for each plot separately in brackets.

### VIII. SUMMARY

1. The situation, geology and general climate of Budongo forest are described. The mean annual rainfall on the edge of the forest is about 1500 mm. (59 in.).

2. Brief mention is made of the main biotic factors affecting the area. Until recently man has had a negligible influence on the forest, but elephant and fire play a major part in controlling development.

3. The forest is comparatively young. Although it is spreading it is unable to colonize pure stands of elephant grass.

4. The least advanced type of closed forest at Budongo is Colonizing Forest, in which one associates and one consociates are recognized. Colonizing Forest is succeeded by Mixed Forest and Mixed Forest is succeeded by Ironwood Forest, which is the climatic climax. Swamp Forest is regarded as an edaphic climax. Both climaxes are consociations.

5. An account is given of the methods used to investigate the forest. Floristic composition was studied in eleven sample plots each 122 m. (400 ft.) square. Structure is illustrated by means of profile diagrams constructed from data from clear-felled plots.

6. Colonizing Forest is shown to be two-storied, Mixed Forest four-storied and Ironwood Forest three-storied. The stratification of Ironwood Forest and of Mixed Forest differ only in the fact that in Ironwood Forest the topmost (emergent) layer is composed almost entirely of the same tree (*Cynometra alexandri* C. H. Wright) which dominates the main canopy. In Mixed Forest the two top layers are composed of different species.

7. Shrub and herb strata are described. Climbers, epiphytes, parasites and saprophytes are discussed.

8. A description of the forest types is followed by a comparison of Budongo with other forests in Uganda and with rain forests elsewhere in the tropics. The climax type at Budongo is shown to have a close general similarity with consociations described from British Guiana, although fewer understory species are present.

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Table 10. Sample Plot 1. Colonizing (Woodland) Forest

Species	Diameter class							Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)			
<i>Albizia zygia</i> Macbride	7	—	—	—	—	1	7	1	—
<i>Antidesma laciniatum</i> Muell. Arg. var. <i>membranaceum</i> Muell. Arg.	3	—	—	—	—	—	3	—	—
<i>Aphania senegalensis</i> Radlk.	71	44	15	1	—	—	131	—	—
<i>Calocoba schweinfurthii</i> Gilg	21	2	—	—	—	—	23	—	—
<i>Celtis brownii</i> Rendle	4	2	—	1	—	—	7	—	—
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	2	2	1	1	—	1	7	—	—
<i>C. kraussiana</i> Bernh.	1	—	—	—	—	—	1	—	—
<i>C. zenkeri</i> Engl.	1	—	—	—	—	—	1	—	—
<i>Chrysophyllum albidum</i> G. Don	4	—	—	—	—	—	4	—	—
<i>Clausena anisata</i> Oliv.	—	—	—	1	—	—	1	—	—
<i>Cleistanthus patens</i> Engl. & Diels	—	—	—	—	—	—	—	—	—
<i>Cordia millenii</i> Baker	—	—	—	—	—	—	—	—	—
<i>Ocotea macrostachys</i> Hochst. ex A. Rich.	—	—	—	—	—	—	—	—	—
<i>Dombeya mukole</i> Sprague	8	—	—	—	—	—	9	—	—
<i>Ehretia cymosa</i> Thonn.	—	1	—	—	—	—	1	—	—
<i>Erythrophloeum guineense</i> G. Don	12	1	2	—	—	—	15	—	—
<i>Fagara angolensis</i> Engl.	—	—	1	—	—	—	1	—	—
<i>Funtumia elastica</i> Stapf	—	—	—	—	—	—	—	—	—
<i>Lannea veluticarpa</i> Engl.	1	—	—	—	—	—	1	—	—
<i>Lepidodermis lauriflorus</i> Benth.*	28	5	—	—	—	—	33	—	—
<i>Linociera johnsonii</i> Baker	1	—	—	—	—	—	1	—	—
<i>Maba abyssinica</i> Hiern	15	1	—	1	—	—	17	—	—
<i>Markhamia platycalyx</i> Sprague	—	—	—	—	—	—	—	—	—
<i>Morus lactea</i> Mildbr.	1	—	—	—	—	—	1	—	—
<i>Olea veluticarpa</i> Gilg & Schellenb.	17	11	7	6	3	—	48	13	—
<i>Phyllanthus discoides</i> Muell. Arg.	6	—	5	4	1	—	19	8	—
<i>Phytolophum abyssinicum</i> Del.	2	2	—	—	—	—	4	—	—
<i>Premna angolensis</i> Guerte	2	—	—	1	—	—	3	—	—
<i>Sapium ellipticum</i> Pax	1	—	3	2	2	—	14	10	—
<i>Spathodea campanulata</i> Beauv.	5	4	8	4	2	—	23	6	—
<i>Tapura fischeri</i> Engl.	2	—	—	—	—	—	2	—	—
<i>Teclea nobilis</i> Del.	3	1	—	—	—	—	4	—	—
<i>Terminalia velutina</i> Rolfe	—	3	11	8	1	—	26	12	—
<i>Tournefortia floribunda</i> Hochst.	35	4	1	—	—	—	40	—	—
<i>Uvariopsis</i> n.sp.? (E. 2291)	21	—	—	—	—	—	21	—	—
35 species	274	85	54	30	12	18	473	60	—

\* This species, which occurs in several S.P.'s, is more often a scandent shrub than a tree.

## (b) Shrub layer

A confused jumble of immature small trees and shrubby undergrowth with *Lepidoturus* the most abundant species, forming local coppice-like thickets.

<i>Acalypha</i> spp.	f.
<i>Alaphyllus velutinosus</i> Gilg (E.sn.)	f.
<i>Belonophora glomerata</i> M. B. Moss	r.
<i>Capparis azevii</i> Pax	o.
<i>Clerodendron capitatum</i> Schum. & Thonn. (E.sn.)	o.
<i>Coffea eugenioides</i> S. Moore (E. 1455)	f.
<i>Ficus urceolaris</i> Welw. ex Hiern	f.
<i>Grewia pubescens</i> Beauv. (E. 2018)	o.
<i>Holoptelea grandis</i> Mildbr.	r. (saplings)
<i>Lepidoturus latiflorus</i> Benth.	a.
<i>Ochna</i> n.sp. (E. 2265)	o.
<i>Pavetta insignis</i> Brém. (E. 3621)	o.
<i>Poponia itoraitis</i> Bagsh. & Bak. f. (E. 2003)	f.
<i>Psychotria</i> sp. (E. 2321)	o.
<i>Psychotria</i> sp. (E.sn.)	f.
<i>Taranea pavettoides</i> Sim (E. 3146)	o.
<i>Trymatococcus kamerianus</i> Engl. (E.sn.)	o.

Also many dwarfed plants of *Clausena anisata*, *Tapura fischeri*, *Tectea nobilis*, etc.

## (c) Herbs

Main cover provided by Acanthaceae but much local variation. No ferns.

## (i) Dicotyledons:

<i>Acalypha</i> spp.	a.
Acanthaceae (various)	a.
<i>Achyranthes aspera</i> Linn. (E. 2286)	f.-v.f.
<i>Cyathula prostrata</i> Bl. (E. 5113)	f.
<i>Hibiscus calyphyllus</i> Cav. (E. 69)	f.

## (ii) Monocotyledons:

<i>Asparagus</i> sp. (E.sn.)	r. (gaps)
<i>Olyra latifolia</i> Linn. (E. 1413)	f.-l.a.
<i>Opismenus hirtellus</i> Beauv. (E. 2287)	o.
<i>Scleria chenabieri</i> Stapf & C. E. Hubbard (E. 2301)	o.-r.
<i>Rotbortia exaltata</i> Linn. f. (E. 4357)	r. (gaps)

## (d) Climbers

At least 14 medium-large climbers; numerous smaller climbers; many herbaceous twiners. A few relic *Toddalia asiatica* Lam. (E. 281) in gaps (see also description of P.P. 1, p. 26).

## (e) Parasites

None

## (f) Epiphytes

Epiphytic orchids very few, confined to one or two of the largest trees and to dying *Terminalia*. About 7-8 species of epiphytic ferns.

## (g) Timber regeneration

Many seedlings of *Albizia zygia*. Two small saplings of *Chrysophyllum albidum*; one sapling of *Entandrophragma utile*.



Table 11. Sample Plot 2. Colonizing (*Maesopsis*) Forest

Species	(a) Trees 10 cm. (4 in.) diameter and over						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	Diameter class							
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Antidesma laciniatum</i> Muell. Arg. var. <i>membranaceum</i> Muell. Arg.	—	—	1	—	—	—	1	—
<i>Belonophora glomerata</i> M. B. Moss*	1	—	—	—	—	—	1	—
<i>Bombax reflexum</i> Sprague	1	—	—	—	—	—	1	—
<i>Caloncoba schweinfurthii</i> Gilg	157	91	8	—	—	—	256	—
<i>Candellum vulgare</i> Bullock	—	2	—	—	—	—	2	—
<i>Cassia mannii</i> Oliv.	—	—	1	—	—	—	1	—
<i>Celtis brownii</i> Rendle	2	—	—	—	—	—	2	—
<i>C. kraussiana</i> Bernh.	—	1	—	—	—	—	1	—
<i>Chrysophyllum albidum</i> G. Don	—	1	—	—	—	—	1	—
<i>Cordia millenii</i> Baker	—	2	2	1	—	—	5	1
<i>Dactyandra arborescens</i> Welw. ex Benth. & Hook. f.	1	—	—	—	—	—	1	—
<i>Dombeya nobile</i> Sprague	5	—	—	—	1	—	6	—
<i>Erythrophileum guineense</i> G. Don	15	5	4	1	—	—	25	1
<i>Fagara angolensis</i> Engl.	1	—	—	—	—	—	1	—
<i>Funtumia elastica</i> Stapf	3	—	1	—	—	—	4	—
<i>Gelonium zanzibarense</i> Muell. Arg.	2	—	—	—	—	—	2	—
<i>Holoptelia grandis</i> Mildbr.	1	—	—	—	—	—	1	—
<i>Klainedoxa gabonensis</i> Pierre	—	1	—	—	—	—	1	—
<i>Lepidolobus latiflorus</i> Benth.	7	—	—	—	—	—	7	—
<i>Linociera johnsonii</i> Baker	1	1	—	—	—	—	2	—
<i>Maba abyssinica</i> Hiern	3	—	—	—	—	—	3	—
<i>Maesopsis eminii</i> Engl.	1	9	20	27	5	2	64	34
<i>Markhamia platycalyx</i> Sprague	3	1	—	—	—	—	4	—
<i>Morus lactea</i> Mildbr.	2	—	—	—	—	—	2	—
<i>Ocotea tenuissima</i> Stapf	5	—	—	—	—	—	5	—
<i>Olea welwitschii</i> Gilg & Schellenb.	15	18	24	10	2	—	69	12
<i>Phyllanthus discoides</i> Muell. Arg.	5	10	14	3	1	—	33	4
<i>Prenna angolensis</i> Guerte	2	3	—	—	—	—	5	—
<i>Sapium ellipticum</i> Pax	1	9	4	4	—	—	18	4
<i>Spathodea campanulata</i> Beauv.	2	4	4	1	1	—	12	2
<i>Tapura fischeri</i> Engl.	2	1	—	—	—	—	3	—
<i>Terminalia velutina</i> Rolfe	1	6	1	—	—	—	8	—
<i>Tournea floribunda</i> Hochst.	4	—	—	—	—	—	4	—
<i>Uvariopsis</i> n.sp.? (E. 2291)	5	—	—	—	—	—	5	—
34 species	248	165	84	47	10	2	556	59

\* Normally shrubby.

## (b) Shrub layer

Layer composed chiefly of immature understory trees. True shrubs few.

<i>Argemuellera macrophylla</i> Pax (E. 1563)	f.
<i>Celtis brownii</i> Rendle	f.
<i>Clausena anisata</i> Oliv.	f.
<i>Doryalis abyssinica</i> Warb.	f.
<i>Grevia pubescens</i> Beauv. (E. 2018)	o.
<i>Lepidodermis lauriflorus</i> Benth.	a.
<i>Maba abyssinica</i> Hiern	f.
<i>Mimocylon jasminoides</i> Gilg (E. 1984)	o.
<i>Pavetta insignis</i> Brém. (E. 3621)	v.f.
<i>Psychotria</i> sp. (E.sn.)	v.f.
<i>Rauvolfia vomitoria</i> Afz.	o.
<i>Rinorea ardisiaeflora</i> O. Ktze.	f.
<i>Tarenna paretoides</i> Sim (E. 3146)	f.
<i>Teclea nobilis</i> Del.	f.

## (c) Herbs

Main cover provided by small Acanthaceae (especially *Pseuderanthemum*) and by *Optismenus hirtellus* Beauv. (E. 2287). *Hibiscus calyphyllus* Cav. (E. 69) the only frequent large herb. Besides *Optismenus*, three other grasses occur: *Streptogyne gerontogaea* Hook. f. (E. 5179), in small patches; *Olyra latifolia* Linn. (E. 1413), occasional; and a few tufts of *Setaria chevalieri* Stapf ex Stapf & C. E. Hubbard (E. 2301). Other monocotyledons very rare. No ferns.

## (d) Climbers

True lianas absent; strong soft-stemmed climbers frequent; herbaceous climbers very abundant. Three species attain 24 m. (80 ft.); the majority less than 9 m. (30 ft.). Species include *Abrus pulchellus* Wall. (E.sn.), *Afromendocia gilgiana* Lindau (E.sn.), *Artabotrys nitidus* Engl. (E. 431), *Bucineria africana* Mast. (E. 3835), *Cissus dubia* Becc. (E.sn.), *Clerodendron capitatum* Sch. & Thonn. (E.sn.), *Combretum rhodanthum* Engl. & Diels (E. 1602), *Hippocratea* spp., *Ipomoea* spp., *Paullinia pinnata* Poir. (E. 140), *Popocia littoralis* Bagn. & Bak. f. (E. 2003), *Rutidea smithii* Hiern (E. 33), *Tetracera potatoria* Afz. (E. 450), and *Tragia brevipetala* Pax (E. 56).

## (e) Epiphytes

Epiphytic orchids few (about 10 species), including *Aerangis rhodosticta* Schltr. (E. 2185), fairly common on stems of small trees. *Platygyrium angolense* Welw. (E. 5478) the only common epiphytic fern.

## (f) Parasites

None

## (g) Timber regeneration

A few small saplings of *Chrysophyllum albidum* and *C. perpulchrum*; several young *Ectandrophragma utile*, to 1 m. (3 ft.); numerous small sapling *Erythrophloeum guineense*.

Table 12. Sample Plot 3. Colonizing (Maesopsis) Forest

Species	Diameter class						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Alstonia congensis</i> Engl.	5	—	2	—	—	2	9	2
<i>Antrocarpon microstera</i> A. Chev. & Guill.	1	—	1	—	—	—	2	—
<i>Balanocitrus dawei</i> Stapf	1	—	—	—	—	—	1	—
<i>Caloncoba schweinfurthii</i> Gilg	33	32	8	—	—	—	73	—
<i>Candium vulgare</i> Bullock	115	6	1	—	—	—	1	—
<i>Celtis brounii</i> Rendle	13	7	—	—	—	—	121	—
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	—	2	—	—	—	—	20	—
<i>C. zenkeri</i> Engl.	1	—	—	—	—	—	2	—
<i>Chaetacme microcarpa</i> Rendle	9	7	—	—	—	—	1	—
<i>Chrysophyllum albidum</i> G. Don	4	—	—	—	—	—	16	—
<i>Conopharyngia holstii</i> Stapf	—	—	—	—	—	—	4	—
<i>Cordia millenii</i> Baker	—	—	—	1	2	—	3	3
<i>Dombeya mukole</i> Sprague	—	1	1	—	—	—	2	—
<i>Ehretia cymosa</i> Thonn.	—	3	2	—	—	—	5	—
<i>Erythrophloeum guineense</i> G. Don	4	1	—	—	1	—	6	1
<i>Fagara angolensis</i> Engl.	—	1	—	—	—	—	1	—
<i>Funtumia elastica</i> Stapf	28	4	—	2	—	—	34	2
<i>F. latifolia</i> Stapf ex Schltr.	1	19	5	—	—	2	27	2
<i>Gelonium zanzibarense</i> Muell. Arg.	5	—	—	—	—	—	5	—
<i>Guarea cedrata</i> Pellegrin	3	—	—	—	—	—	3	—
<i>Holoptelea grandis</i> Mildbr.	14	4	1	—	2	—	21	2
<i>Klaineodoza gabonensis</i> Pierre	—	1	—	—	—	—	1	—
<i>Maba abyssinica</i> Hiern	147	4	—	23	25	26	147	74
<i>Maesopsis eminii</i> Engl.	1	3	6	—	—	—	84	—
<i>Morus lactea</i> Mildbr.	—	—	2	—	—	—	6	—
<i>Ocotea tenuissima</i> Stapf	26	10	—	—	—	—	1	—
<i>Olea velutischi</i> Gilg & Schellenb.	1	—	—	—	1	—	37	1
<i>Pavetta insignis</i> Brém. (E. 3821)*	5	—	—	—	—	—	1	—
<i>Phyllanthus discoides</i> Muell. Arg.	—	7	8	11	1	—	32	12
<i>Premna angolensis</i> Guérke	33	1	1	—	—	—	2	—
<i>Pterygota</i> n.sp. (E. 1609)	—	5	2	—	—	—	40	—
<i>Randia malleifera</i> Benth. & Hook. f.	1	—	1	2	1	—	1	—
<i>Saprium ellipticum</i> Pax	—	1	1	—	—	—	5	3
<i>Spathodea campanulata</i> Beauv.	3	3	1	1	1	—	9	2
<i>Tapura fischeri</i> Engl.	23	1	—	—	—	—	25	1
<i>Tectea nobilis</i> Del.	—	5	1	—	—	—	6	—
<i>Uvariopsis</i> n.sp.? (E. 2291)	2	3	—	—	—	—	6	—
<i>Vangueria acutiloba</i> Robyns*	2	—	—	—	—	—	2	—
38 species	481	132	44	41	34	30	762	105

\* Perhaps better regarded as shrubs.

## (b) Shrub layer

Layer composed chiefly of young individuals of (a) *Celtis brounii*, (b) *Maba abyssinica*, (c) *Psychotria* sp., and (d) other shrubs and immature trees, in the proportions, roughly, 1:1:1:2.

- Allophylus welchii* Gilg (E.sn.) f. (to 1 m.)  
*Capparis afzelii* Pax a.  
*Celtis brounii* Rendle v.f. (all small)  
*Clatsena anisala* Oliv. f.  
*Coffea eugenoides* S. Moore (E. 1455) o.  
*Doryalis macrocalyx* Warb. (E. 62) f. (to 1 m.)  
*Lepidodermis laxiflorus* Benth. a. (few under 2 m.)  
*Maba abyssinica* Hiern o.  
*Ochna* n.sp. (E. 2265) a. (to 4 m.)  
*Psychotria* sp. (E.sn.) o.  
*Randia ureliformis* Hiern f. (to 2 m.)  
*Rinorea poggii* Engl. f. (to 1 m.)  
*Teclea nobilis* Del.

## (c) Herbs

## (i) Dicotyledons:

- Achyranthes aspera* Linn. (E. 2286) v.f.  
*Brilliantaisia* sp. (E. 2290) f.  
*Geophila uniflora* Hiern (E. 433) f.  
*Justicia glabra* Roxb. (E. 943) v.f.-a  
*Pseuderanthemum tunicatum* Milne-Redhead (E. 2273)

## (ii) Monocotyledons:

- Bufoerestia* n.sp.? (E. 1414) f.  
*Calanthe corymbosa* Lindl. (E. 2106) o.

*Commelinidum mayumbense* Stapf (E. 4483)

- Leptaspis cochleata* Thwaites (E. 3329) f.  
*Marantochloa* sp. (E.sn.) o.  
*Olyra latifolia* Linn. (E. 1413) o.  
*Opismenus hirtellus* Beauv. (E. 2287) v.f.  
*Setaria chevalieri* Stapf ex Stapf & C. E. Hubbard (E. 2301) f.  
*Streptogyne gerontogaea* Hook. f. (E. 5179) a. (dominant)

## (iii) Ferns:

- Doryopteris concolor* Kuhn (E. 2026) f.  
*Pteris tripartita* Sw. (E. 1469) f.

## (d) Climbers

At least twenty-four medium-sized lianas; a few large climbers and many small.

## (e) Epiphytes

Very few epiphytic orchids. A few tufts of *Platygerium angolense* Welw. (E. 5478).

## (f) Parasites

None

## (g) Timber regeneration

*Albizia zygia* the only large tree with much seedling regeneration; also a few plants to 0.3 m. (1 ft.). One plant of *Chrysophyllum albidum* 1.2 m. (4 ft.) and one of *Entandrophragma utile* 0.6 m. (2 ft.). Abundant regeneration (all sizes) of *Celtis brounii*. Many *Teclea nobilis* and *Tapura fischeri* to 1 m. (3 ft.). *Maba abyssinica* not regenerating.

Table 13. Sample Plot 4. Ecotone between Colonizing (Maesopsis) Forest and Mixed Forest

Species	Diameter class						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Albizia coriaria</i> Welw.	—	—	1	—	1	—	2	1
<i>A. zygia</i> Macbride	—	—	—	—	—	3	3	3
<i>Astonia congensis</i> Engl.	—	—	1	—	—	1	2	1
<i>Aphania senegalensis</i> Radlk.	4	2	—	—	—	—	6	—
<i>Caloncoba schweinfurthii</i> Gilg	2	1	—	—	—	—	3	—
<i>Cassipourea ugandensis</i> Alston	41	6	1	—	—	—	48	—
<i>Celtis brownii</i> Rendle	6	1	6	—	—	—	13	—
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	9	4	—	—	—	—	13	—
<i>C. soyauxii</i> Engl.	5	4	3	1	1	2	16	4
<i>C. zenkeri</i> Engl.	—	—	—	1	—	—	1	1
<i>Chlorophora excelsa</i> Benth. & Hook. f.	2	—	—	—	—	—	2	—
<i>Chrysophyllum albidum</i> G. Don	2	1	—	—	—	—	3	—
<i>C. glomeruliferum</i> Hutch. & J. M. Dalz.	1	—	1	—	—	—	2	—
<i>C. perpulchrum</i> Mildbr. ex Hutch. & J. M. Dalz.	2	—	—	—	—	—	2	—
<i>Clausena anisata</i> Oliv.	1	—	—	1	—	—	2	—
<i>Cleistanthus patens</i> Engl. & Diels	1	—	—	—	—	—	2	—
<i>Cola cordifolia</i> R. Br.	1	1	—	—	—	—	3	—
<i>Conopharargyia holstii</i> Stapf	67	8	—	—	—	1	75	1
<i>Cordia millenii</i> Baker	1	—	—	—	—	—	1	—
<i>Drypetes ugandensis</i> Hutch. (E. 3078)	4	1	—	—	—	—	5	—
<i>Ehretia cymosa</i> Thonn.	1	—	—	—	—	—	1	—
<i>Entandrophragma cylindricum</i> Sprague	—	—	1	—	—	—	1	—
<i>Erythrophileum guineense</i> G. Don	2	1	—	—	—	2	5	2
<i>Fagaropsis angolensis</i> Greenway	1	—	—	—	—	—	1	—
<i>Flacourtia ramontchi</i> L'Hérit.	—	1	—	—	1	—	2	1
<i>Funtumia elastica</i> Stapf	3	1	—	—	—	—	4	—
<i>F. latifolia</i> Stapf ex Schltr.	53	68	37	9	2	—	169	11
<i>Gelonium zanzibarense</i> Muell. Arg.	3	—	—	—	—	—	3	—
<i>Khaya anthotheca</i> C.DC.	—	—	—	—	—	1	1	1
<i>Klainedoxa gabonensis</i> Pierre	2	1	—	—	—	—	3	—
<i>Lepidoloturus laxiflorus</i> Benth.	43	1	—	—	—	—	44	—
<i>Leptonychia multiflora</i> K. Schum.	1	—	—	—	—	—	1	—
<i>Maba abyssinica</i> Hiern	2	—	—	—	1	—	3	1
<i>Maesopsis eminii</i> Engl.	—	—	—	3	4	20	27	27
<i>Majidea (Harpullia) fosteri</i> Sprague	—	1	—	—	—	—	1	—
<i>Markhamia platycalyx</i> Sprague	—	1	—	—	—	—	1	—
<i>Melanodiscus</i> n.sp.? (E. 3451)	—	1	—	—	—	—	1	—
<i>Milbrandtia excelsa</i> Harms	1	—	—	—	—	—	1	—
<i>Morus lactea</i> Mildbr.	3	—	—	—	—	—	3	—
<i>Myrianthus arboreus</i> Beauv.	13	2	—	1	—	—	16	1
<i>Olea veluticarpa</i> Gilg & Schellenb.	6	8	7	4	5	1	31	10
<i>Oryzanthus speciosus</i> DC.*	1	—	—	—	—	—	1	—
<i>Pavetta insignis</i> Brém. (E. 3621)*	1	—	—	—	—	—	1	—
<i>Phyllanthus discoides</i> Muell. Arg.	9	6	8	8	—	1	32	9
<i>Piptadenia africana</i> Hook. f.	—	—	—	—	—	1	1	1
<i>Premna angolensis</i> Guertke	1	—	—	—	1	1	3	2

(a) Trees 10 cm. (4 in.) diameter and over

<i>Pygeum africanum</i> Hook. f.	1	1	2	—	1	2	7	3
<i>Rinorea ardisiaeflora</i> O. Ktze.	4	1	—	—	—	—	5	—
<i>Sapium ellipticum</i> Pax	1	2	2	2	1	—	8	3
<i>Spathodea campanulata</i> Beauv.	1	1	1	—	1	—	4	1
<i>Sterculia dawsoni</i> Sprague	—	—	—	—	—	1	1	1
<i>Tapara fischeri</i> Engl.	4	—	—	—	—	—	4	—
<i>Teclea nobilis</i> Del.	1	—	—	—	—	—	1	—
<i>Tetrapleura tetraptera</i> Taub.	—	—	—	—	—	—	1	—
<i>Trichilia heudelotii</i> Planch.	169	12	—	1	—	—	181	1
<i>T. prieuriana</i> A. Juss.	1	—	1	—	—	—	2	—
<i>Uvariopsis</i> n.sp.? (E. 2291)	2	—	—	—	—	—	2	—
<i>Vitex amboniensis</i> Guertke	2	—	—	—	—	—	2	—
58 species	480	139	72	31	19	37	778	87

\* Usually shrubby.

## (b) Shrub layer

Many unidentified stunted woody species 0.3–1 m. (1–3 ft.).

<i>Coffea eugenoides</i> S. Moore (E. 1455)	o.
<i>Conopharyngia holstii</i> Stapf	o.
<i>Lepidodermis lauriflorus</i> Benth.	l.a. (mostly dwarfed)
<i>Microdesmis zenkeri</i> Pax	o.
<i>Ochna</i> n.sp. (E. 2265)	o.
<i>Ouratea densiflora</i> De Wild. & Dur. (E. 1179)	o.
<i>Oxyanthus</i> spp.	o.
<i>Ptilosporum abyssinicum</i> Del.	r. (small)
<i>Popowia littoralis</i> Bagn. & Bak. f. (E. 2003)	o.
<i>Psychotria</i> spp.	o. (small)
<i>Teclea nobilis</i> Del.	o. (small)
<i>Trichilia heudelotii</i> Planch.	f.
<i>Uvariopsis</i> n.sp.? (E. 2291)	a.

## (c) Herbs

## (i) Dicotyledons:

<i>Geophila uniflora</i> Hiern (E. 433)	f.
<i>Pseuderanthemum tunicatum</i> Milne-Redhead (E. 2273)	o.

## (ii) Monocotyledons:

Araceae (indet.)	r.
<i>Lepidaspis cochleata</i> Thwaites (E. 3320)	v.a. (dominant)
<i>Oliva latifolia</i> Linn. (E. 1413)	o.
<i>Streptogyne gerontogaea</i> Hook. f. (E. 5170)	o.

## (iii) Ferns:

Two species (desiccated; not identified)

## (d) Climbers

A few twiners and taller climbers. At least thirty-eight lianas.

## (e) Epiphytes

Not abundant, mostly confined to a few old trees.

<i>Asplenium africanum</i> Desv. (E. 2109)
<i>Platycerium angolense</i> Welw. (E. 5478)
<i>Polypodium phymatodes</i> Linn. (E. sn.)
<i>Polystachya</i> spp. (two)
<i>Rhipidoglossum rutitum</i> Schltr. (E. 2226)
<i>Rhipsalis cassipha</i> Gaertn. (E. 2171)

## (f) Parasites

None

## (g) Timber regeneration

Saplings of Mixed Forest species noticeable, especially in older part of plot, including *Chrysophyllum albidum* (two), *C. perpulchrum* (one), *Cymometra alexandri* (four), *Entandrophragma cylindricum* (two), *E. utile* (one), *Khaya anthotheca* (one). Many small *Celtis soyaurii*. Some seedlings of *Albizia zygia*. No *Funtumia* regeneration.

Table 14. Sample Plot 5. Mixed Forest

Species	(a) Trees 10 cm. (4 in.) diameter and over						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Albizia zygia</i> Macbride	3	—	—	—	1	—	2	—
<i>Allophylus</i> sp. (E. 3970)	1	—	—	1	2	5	10	8
<i>Astonia congensis</i> Engl.	1	1	—	—	—	—	2	—
<i>Antingeria altissima</i> Aubr. & Pellegrin	1	—	—	—	—	—	1	—
<i>Baphia vollettii</i> Bak. f.	1	—	—	—	—	—	1	—
<i>Belonophora glomerata</i> M. B. Moss*	1	—	—	—	—	—	1	—
<i>Blighia wilsoniana</i> Gilg & Radlk.	—	—	—	—	—	—	—	—
<i>Bosquicia phobos</i> Baill.	—	9	6	1	—	—	16	1
<i>Celtis brownii</i> Rendle	105	25	2	3	1	—	132	4
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	166	52	17	2	—	—	237	2
<i>C. soyauzii</i> Engl.	7	7	4	—	—	—	18	—
<i>C. zenkeri</i> Engl.	4	4	—	—	—	—	8	—
<i>Chadacme microcarpa</i> Rendle	—	—	—	—	—	—	—	—
<i>Chlorophora excelsa</i> Benth. & Hook. f.	—	1	—	—	—	1	2	1
<i>Chrysophyllum albidum</i> G. Don	5	2	3	2	2	—	15	5
<i>C. glomeruliferum</i> Hutch. & J. M. Dalz.	—	1	1	—	—	—	2	—
<i>C. perpulchrum</i> Mildbr. ex Hutch. & J. M. Dalz.	5	6	2	1	2	1	17	4
<i>Chrysophyllum</i> n.sp.? (E. 2248)	4	5	3	1	2	6	21	9
<i>Coffea canephora</i> Pierre*	1	—	—	—	—	—	1	—
<i>Cola cordifolia</i> R.Br.	—	1	—	1	1	—	3	2
<i>Connarus longistipitatus</i> Gilg.	2	—	—	—	—	—	2	—
<i>Conopharyngia holstii</i> Stapf.	5	—	—	—	—	—	5	—
<i>Cordia millenii</i> Baker	—	1	—	—	—	1	2	1
<i>Craterispermum laurinum</i> Benth.	1	—	—	—	—	—	1	—
<i>Cynometra alexandri</i> C. H. Wright	7	3	2	1	—	—	14	2
<i>Dialium</i> sp. prob. <i>D. dipendense</i> Harms. (E. 2136)	1	—	—	—	—	—	1	—
<i>Drypetes ugandensis</i> Hutch. (E. 3078)	3	2	—	—	—	—	5	—
<i>Entandrophragma cylindricum</i> Sprague	—	—	—	—	—	3	3	—
<i>E. utile</i> Sprague	1	—	—	—	—	—	1	—
<i>Erythrina excelsa</i> Baker	—	—	1	—	—	—	1	—
<i>Erythrophloeum guineense</i> G. Don	1	—	—	—	—	—	1	—
<i>Fagaropsis angolensis</i> Greenway	—	—	—	—	—	3	4	3
<i>Funtumia elastica</i> Stapf	9	16	1	1	1	—	36	2
<i>Gelonium zambianense</i> Muell. Arg.	3	—	8	3	—	—	3	3
<i>Guarea cedrata</i> Pellegrin	1	—	—	1	—	—	2	—
<i>Holoptelea grandis</i> Mildbr.	—	—	—	1	1	—	2	2
<i>Khaya anthotheca</i> C.DC.	—	—	—	1	1	—	2	2
<i>Klaineodoxa gabonensis</i> Pierre	—	—	—	1	—	—	1	—
<i>Laccodiscus</i> n.sp. (E. 1140)	1	—	—	—	—	—	1	—
<i>Lepidoturus laxiflorus</i> Benth.	22	—	—	—	—	—	22	—
<i>Madia (Harpulia) fosteri</i> Sprague	1	1	2	—	—	—	4	—
<i>Markhamia platyacalyx</i> Sprague	—	1	—	—	—	—	1	—
<i>Microdiscus</i> n.sp.? (E. 3451)	17	18	4	3	1	—	43	4
<i>Mimusops ugandensis</i> Stapf	1	2	—	—	—	—	3	—
<i>Morinda lucida</i> Benth.	—	—	1	1	—	—	2	1
<i>Morus lactea</i> Mildbr.	1	—	1	—	—	—	1	1
<i>Myrsine arborea</i> Beauv.	1	—	1	—	—	—	2	—
<i>Phyllanthus discoides</i> Muell. Arg.	—	1	—	1	—	—	2	—
<i>P. inflatus</i> Hutch.	1	—	—	—	—	—	1	—
<i>Randia urecliformis</i> Hieron.*	1	—	—	—	—	—	1	—





Table 15. Sample Plot 6. Mixed Forest

(a) Trees 10 cm. (4 in.) diameter and over\*

Species	Diameter class						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Allophylus</i> sp.†	1	—	—	—	—	—	1	—
<i>Alstonia congenensis</i> Engl.	—	—	—	1	1	8	10	—
<i>Aningeria altissima</i> Aubr. & Pellégrin	2	2	1	2	—	—	7	—
<i>Antiaris toxicaria</i> Lesch.	—	—	—	—	—	2	2	—
<i>Aphania senegalensis</i> Radlk.	—	1	—	—	—	—	1	—
<i>Baphia vollenkii</i> Bak. f.	2	—	—	—	—	—	2	—
<i>Bosqueia phoberos</i> Baill.	18	7	4	1	—	—	30	—
<i>Capparis afzelii</i> Pax	7	1	—	—	—	—	8	—
<i>Celtis brownii</i> Rendle	13	2	—	—	—	—	15	—
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	1	2	—	—	—	—	3	—
<i>C. soyauzii</i> Engl.	164	41	11	—	—	—	216	—
<i>C. zenkeri</i> Engl.	5	3	1	—	—	—	9	—
<i>Chadacme microcarpa</i> Rendle	1	—	—	—	—	—	1	—
<i>Chrysophyllum albidum</i> G. Don	25	9	4	2	3	5	48	—
<i>C. glomeratifolium</i> Hutch. & J. M. Dalz.	15	5	—	—	—	—	20	—
<i>C. perpulchrum</i> Mildbr. ex Hutch. & J. M. Dalz.	6	8	3	2	—	1	20	—
<i>Chrysophyllum</i> n.sp.? (E. 2248)	5	3	2	2	1	3	22	—
<i>Cola cordifolia</i> R.Br.	—	—	—	—	—	—	3	—
<i>Croton megalocarpus</i> Hutch.	1	—	—	—	—	—	1	—
<i>Cynometra alexandrii</i> C. H. Wright	20	11	4	5	4	15	59	—
<i>Dictyandra arborescens</i> Welw. ex Benth. & Hook. f.	2	—	—	—	—	—	2	—
<i>Drypetes</i> sp. prob. <i>D. major</i> Hutch. (E. 3078)	8	—	1	—	—	—	9	—
<i>Entandrophragma cylindricum</i> Sprague	—	2	—	—	—	2	4	—
<i>E. utile</i> Sprague	—	—	2	1	—	—	3	—
<i>Fagara melanacantha</i> Engl.	—	—	—	1	—	—	1	—
<i>Ficus capensis</i> Thunb.	—	—	—	1	—	1	1	—
<i>Funtumia elastica</i> Stapf	4	—	—	—	—	—	4	—
<i>Geonimium zanzibarensis</i> Muell. Arg.	1	—	—	—	—	—	1	—
<i>Glyphaea lateriflora</i> Hutch. & J. M. Dalz.†	2	—	—	—	—	—	2	—
<i>Guarea cedrata</i> Pellegrin	2	1	—	—	—	—	3	—
<i>Holoptelea grandis</i> Mildbr.	—	—	—	—	—	2	2	—
<i>Kaya anthotheca</i> C.DC.	1	1	—	1	2	13	18	—
<i>Klainea gaboensis</i> Pierre	—	1	—	1	—	—	2	—
<i>Laccodiscus</i> n.sp. (E. 1140)	2	1	—	—	—	—	3	—
<i>Lepidoturus lauriflorus</i> Benth.	12	—	—	—	—	—	12	—
<i>Mammea africana</i> Sabine (E. 4979)	1	—	—	—	—	—	1	—
<i>Melanodiscus</i> n.sp.? (E. 3451)	9	5	1	—	—	—	15	—
<i>Mildbraediodendron excelsum</i> Harms	—	—	—	—	—	1	1	—
<i>Mimusops ugandensis</i> Stapf	2	1	1	2	—	—	6	—
<i>Mitragyna stipulosa</i> O. Ktze.	—	1	—	—	—	—	1	—
<i>Myrsine arborea</i> Beauv.	1	3	—	—	—	—	4	—
<i>Parkea filicoides</i> Welw.	1	—	—	—	—	—	1	—
<i>Phyllanthus inflatus</i> Hutch.	1	—	—	—	—	—	1	—
<i>Piptadenia africana</i> Hook. f.	—	—	—	—	—	—	—	—
<i>Pseudospondias microcarpa</i> Engl.	1	—	—	—	1	3	5	—
<i>Retinodendron africanum</i> Muell. Arg.	—	—	—	—	—	1	1	—

*Rinorea ardisiaeflora* O. Ktze.  
*Slaudia* sp.? (E. 4253)  
*Tectia grandifolia* Engl.  
*Tetraphleura tetraphleura* Taub.  
*Trichilia heudelotii* Planch.  
*T. prieuriana* A. Juss.  
*Uvariopsis* n.sp.? (E. 2291)

53 species

\* Of the species listed, the following occur only beside the stream which crosses the plot: *Glyphara lateriflora*, *Parkia filicoides*, *Pseudospondias microcarpa*, and *Mitragyna stipulosa*.  
 † Best regarded as shrubs.

(b) Shrub layer

*Acalypha* spp.  
*Argemuellera macrophylla* Pax (E. 1563)  
*Capparis afzelii* Pax  
*Lepidoturus lauriflorus* Benth.  
*Oryandus speciosus* DC.  
*Rinorea poggei* Engl.  
*Teclea grandifolia* Engl.  
*Whitfieldia elongata* C. B. Cl. (E. 1552)

(c) Herbs

(i) Dicotyledons:  
 Acanthaceae (several spp. other than the two following;  
 chiefly small *Whitfieldia*) f.  
*Justicia glabra* Roxb. (E. 1943) o.  
*Mellera lobulata* S. Moore (E. 1476) o.  
*Piper umbellatum* Linn. (E. 404) r.-o.

(ii) Monocotyledons:

*Aframomum* sp. (E.sn.) o.  
*Corymbis welitschii* Rehb. f. (E. 3396) o.-f.  
*Dracaena fragrans* Ker-Gawl. (E. 1423) r.-o. (0.5 m.)  
*Leptaspis cochleata* Thwaites (E. 2329) f.-la.  
*Olyra latifolia* Linn. (E. 1413) o.  
*Palisota schweinfurthii* C.B.Cl. (E. 2011) r.-o.  
*Pollia condensata* C.B.Cl. (E.sn.) o.  
*Streptogone gerontogara* Hook. f. (E. 5179) o.  
 Zingiberaceae (indet.) r.-o.

(iii) Ferns:

*Asplenium macrophlebium* Baker (E. 2098 A.) o.  
*Asplenium* sp. indet. v.f.

9 — — — — — 9 — —  
 1 — — — — — 1 — —  
 1 — — — — — 2 — —  
 1 — — — — — 2 — —  
 4 — — — — — 6 — —  
 2 — — — — — 12 — —  
 3 — — — — — 3 — —  
 357 117 42 22 12 67 617 101

*Dryopteris mollis* Hieron. (E.sn.) o.  
*Dryopteris* sp. o.  
*Pteris tripartita* Sw. (E. 1469) o.

(d) Climbers

At least seventy lianas (twenty small-stemmed), including *Combretum* sp. (E. 1502). Species probably similar to those on S.P. 5. A few *Culcasia scandens* Beauv. (E.sn.). A few young *Acacia pennata* Willd. to 1 m. (3 ft.).

(e) Epiphytes

Epiphytes not studied in detail, apparently very similar to those on S.P. 5. Several *Tectaria anglicifolia* Copel (E.sn.) on buttresses. One epiphytic *Ficus depauperata* Sim.

(f) Parasites

None

(g) Timber regeneration

Many seedlings of *Cyrometra*, especially on higher ground. Larger plants well represented, including a few small saplings. Only three *Chrysophyllum* saplings; no seedlings. Occasional saplings of *Funtumia* and *Piptadenia*. A few seedling *Entandrophragma cylindricum*.

*Note.* Trees near the stream bore much more moss on their stems than those elsewhere. They also carried rather different vascular epiphytes, amongst them *Acnistobolus rothschildianus* (O'Brien) (E. 1454), *Angraecum infundibulare* Lindl. (E. 2040) and *Procris laevigata* Blume (E. 2012). The flora of the bed of the stream was likewise very different from the rest of the plot. Typical species growing between (and on) the stones composing it were: *Aframomum* sp. (E.sn.)—abundant to locally subdominant, *Diplazium profliferum* Thouars (E. 2122)—dominant, *Elatostemma orientale* Engl. (E. 1419), *Epithema tenue* C. B. Cl. (E. 2010), *Marantochloa* sp. (E.sn.), etc.

Table 16. Sample Plot 7. Ecotone between Mixed Forest and Ironwood Forest

Species	(a) Trees 10 cm. (4 in.) diameter and over						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	Diameter class							
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Allophylus</i> sp. (E. 3970)*	1	—	—	—	1	7	1	8
<i>Alstonia congenensis</i> Engl.	2	—	—	—	—	—	2	—
<i>Aphania senegalensis</i> Radlk.	30	2	—	—	—	—	32	—
<i>Belonophora glomerata</i> M. B. Moss*	—	1	1	1	—	—	3	1
<i>Bosqueia phoberos</i> Baill.	2	—	1	—	—	—	3	—
<i>Caloncoba schweinfurthii</i> Gilg	1	—	—	—	—	—	1	—
<i>Capparis afzelii</i> Pax	11	1	—	—	—	—	12	—
<i>Celtis brownii</i> Rendle	2	4	2	1	1	2	12	4
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	110	18	2	1	—	—	131	1
<i>C. soyauzii</i> Engl.	14	6	1	3	—	—	24	3
<i>C. zenkeri</i> Engl.	5	—	1	—	—	—	6	—
<i>Chrysophyllum albidum</i> G. Don	3	1	—	—	—	1	5	1
<i>C. perpulchrum</i> Mildbr. ex Hutch. & J. M. Dalz.	2	3	—	1	—	—	6	1
<i>Chrysophyllum</i> n.sp.? (E. 2248)	1	—	—	—	—	—	1	—
<i>Clausena anisata</i> Oliv.	4	—	—	—	—	—	4	—
<i>Conopharyngia holstii</i> Stapf	3	—	—	—	—	—	3	—
<i>Cordia millenii</i> Baker	—	—	—	1	1	—	2	—
<i>Croton oxyptaluis</i> Muell. Arg.	—	—	—	—	—	—	—	—
<i>Cynometra alexandri</i> C. H. Wright	1	2	1	1	—	29	34	2
<i>Drypetes ugandensis</i> Hutch. (E. 3078)	1	—	—	—	—	2	1	2
<i>Endandrophragma cylindricum</i> Sprague	—	—	—	—	—	1	1	1
<i>E. utile</i> Sprague	—	—	1	—	—	—	1	—
<i>Erythrina excelsa</i> Baker	—	—	—	—	—	—	—	—
<i>Erythrophileum guineense</i> G. Don	—	—	—	—	—	—	—	—
<i>Funtumia elastica</i> Stapf	12	13	2	—	—	1	27	1
<i>F. latifolia</i> Stapf ex Schltr.	—	1	—	—	—	—	1	—
<i>Khaya anthotheca</i> C.DC.	1	—	—	1	—	9	11	10
<i>Laccodiscus</i> n.sp. (E. 1140)	2	—	—	—	—	—	2	—
<i>Lasioidiscus mildbraedii</i> Engl.	179	52	5	—	—	—	236	—
<i>Lepidoturus lauriflorus</i> Benth.	20	2	—	—	—	—	22	—
<i>Leptaulus daphnoides</i> Benth.	1	1	—	—	—	—	2	—
<i>Leptonychia multiflora</i> K. Schum.	1	—	—	—	—	—	1	—
<i>Melanodiscus</i> n.sp.? (E. 3451)	—	—	—	—	—	—	—	—
<i>Monodora gibsonii</i> Bullock (ined.)	—	1	—	—	1	—	1	1
<i>Morus lactea</i> Mildbr.	—	1	—	—	—	—	1	—
<i>Myrianthus arboreus</i> Beauv.	—	1	—	—	—	—	1	—
<i>Picralima</i> sp. (E. 3972)	—	—	—	—	—	—	—	—
<i>Premna angolensis</i> Guerke	1	—	—	—	—	—	1	—
<i>Rinorea ardisiaeflora</i> O. Ktze.	51	5	1	—	—	—	57	—
<i>Ritchiea albersii</i> Gilg	1	—	—	—	—	—	1	—
<i>Strombosia grandifolia</i> Hook. f.	—	—	1	—	—	—	1	—
<i>Strychnos</i> sp. (E. 1253)	1	1	1	—	—	—	2	—
<i>Tapura fischeri</i> Engl.	—	1	1	—	—	—	2	—
<i>Teclea grandifolia</i> Engl.	2	—	1	—	—	—	3	—
<i>Trema guineensis</i> Ficalho	1	—	—	—	—	—	1	—

<i>Trichilia heudelotii</i> Planch.	10	4	1	—	—	15	—
<i>T. pruriens</i> A. Juss.	—	—	1	—	1	4	3
<i>Unariopsis</i> n.sp.? (E. 2291)	5	1	—	—	—	6	—
<i>Vitex amboniensis</i> Guertke	—	1	—	—	—	1	—
49 species	464	123	23	10	5	699	69

\* Commoner as shrubs.

(b) Shrub layer							
Much intermingling of shrubs and immature small trees.							
<i>Acalypha</i> sp.	a.-d.						
<i>Argemuellera macrophylla</i> Pax (E. 1563)	f.						
<i>Belonophora glomerata</i> M. B. Moss	f.						
<i>Lepidoturus laciflorus</i> Benth.	a.						
<i>Rinorea poggei</i> Engl.	o.						
(c) Herbs							
<i>Leptaspis</i> nearly everywhere dominant. Acanthaceae (taken together) next abundant and even locally dominant.							
(i) Dicotyledons:							
Acanthaceae (other than those listed below)							
<i>Crossandrella dusenii</i> S. Moore (E. 1410)	a.-l.d.						
<i>Cyathula prostrata</i> Bl. (E. 515)	f.						
<i>Isoglossa runguoides</i> S. Moore (E. 2285)	f.						
<i>Justicia glabra</i> Roxb. (E. 943)	o.						
<i>Melastoma lobulata</i> S. Moore (E. 1557)	o.						
<i>Pseuderanthemum ludovicianum</i> Lindau (E. sn.)	f.						
<i>P. tunicatum</i> Milne-Redhead (E. 2273)	f.						
(ii) Monocotyledons:							
<i>Bufoerestia</i> n.sp.? (E. 1414)	o.						
<i>Calanthe corymbosa</i> Lindl. (E. 2106)	o.						
<i>Floscopa africana</i> C.B.Cl. (E. 2284)	o.						
<i>Haemanthus cinnabarinus</i> Decne. (E. 1197)	o.						
<i>Leptaspis cochleata</i> Thwaites (E. 3329)	a. (dominant)						
<i>Olyra latifolia</i> Linn. (E. 1413)	o.						
<i>Optismenus hirtellus</i> Beauv. (E. 2287)	o.						
<i>Pollia condensata</i> C.B.Cl. (E. sn.)	o.						
(iii) Ferns:							
<i>Doryopteris concolor</i> Kuhn (E. 2026)	o.						
<i>Dryopteris mollis</i> Hieron. (E. sn.)	o.						

(d) Climbers

At least twenty-seven lianas

(e) Epiphytes

A profusion of epiphytic ferns and orchids on several of the old large trees (especially the *Entandrophragma utile*). Only a few identified. At least four species of epiphytic fig.

*Ancistrothyrium ovatus* Summerhayes (E. 3360)

*Angraecum infundibulare* Lindl. (E. 2040)

*Asplenium africanum* Desv. (E. 2109)

*Bulbophyllum falcatum* Rehb. f. (E. 2092)

*Davallia chaerophylloides* Steud. (E. 1561)

*Ficus brachylepis* Welw. ex Hiern

*F. depauperata* Sim.

*F. stipulifera* Hutch.

*F. thonningii* Blume

*Platyserium angolense* Welw. (E. 5478)

*Polypodium phymatodes* Linn. (E. sn.)

*Polystachya stuhlmannii* Kraeuzl. (E. 2173)

*Rhipidoglossum* spp. (at least two)

*Rhysopalis cassytha* Gaertn. (E. 2171)

(f) Parasites

None

(g) Timber regeneration.

Much seedling regeneration of *Cynometra*; abundant seedling regeneration of *Lasiodiscus*. Fair numbers of small plants of *Chrysophyllum* spp. Two sapling *Chrysophyllum perpulchrum*; one sapling *Erythrophloeum*.

Table 17. Sample Plot 8. Ecotone between Mixed Forest and Ironwood Forest

Species	Diameter class						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Albizia zygia</i> Macbride	—	—	—	1	—	—	1	1
<i>Alstonia congenensis</i> Engl.	—	—	1	1	1	4	7	6
<i>Aphania senegalensis</i> Radlk.	2	—	—	—	—	—	2	—
<i>Belonophora glomerata</i> M. B. Moss*	1	—	—	—	—	—	1	—
<i>Capparis afzelii</i> Pax	—	1	—	—	—	—	1	—
<i>Celtis brownii</i> Rendle	29	26	11	2	—	—	68	2
<i>C. durandii</i> Engl. var. <i>ugandensis</i> Rendle	3	2	3	—	1	2	11	3
<i>C. boyaurii</i> Engl.	10	2	5	—	1	1	19	2
<i>C. zenkeri</i> Engl.	1	1	—	1	2	—	6	4
<i>Chrysophyllum albidum</i> G. Don	—	1	—	—	—	—	1	—
<i>C. perpulchrum</i> Mildbr. ex Hutch. & J. M. Dalz.	—	—	—	—	1	2	3	3
<i>Chrysophyllum</i> n.sp.? (E. 2248)	—	—	—	—	—	1	1	1
<i>Cynometra alexandri</i> C. H. Wright	9	7	8	4	3	46	77	53
<i>Dialium</i> sp. (E. 3376)	—	—	—	—	1	—	1	1
<i>Funtumia elastica</i> Stapf	2	13	3	—	—	—	18	—
<i>Gelonium zanzibarense</i> Muell. Arg.	2	1	1	—	—	—	4	—
<i>Holoptelea grandis</i> Mildbr.	—	—	—	—	—	2	2	2
<i>Klainedoza gabonensis</i> Pierre	—	—	—	—	—	1	1	—
<i>Lasiodiscus mildbraedii</i> Engl.	—	—	—	—	—	—	—	—
<i>Lepidoturus laxiflorus</i> Benth.	120	81	14	—	—	—	215	—
<i>Majidea (Harpullia) fosteri</i> Sprague	4	1	—	—	—	—	5	—
<i>Melanodiscus</i> n.sp.? (E. 3451)	—	—	—	—	1	—	1	1
<i>Mildbraediodendron excelsum</i> Harms	—	—	1	—	—	—	1	1
<i>Morus lactea</i> Mildbr.	1	—	1	—	—	2	2	2
<i>Myrsine arborea</i> Beauv.	—	—	1	—	—	—	1	—
<i>Phyllanthus discoides</i> Muell. Arg.	—	—	—	—	—	—	—	—
<i>Rinorea ardisiaeflora</i> O. Ktze.	75	8	—	—	—	1	83	—
<i>Tapura fischeri</i> Engl.	5	1	1	—	—	—	7	—
<i>Turraea floribunda</i> Hochst.	1	—	—	—	—	—	1	—
<i>Uvariopsis</i> n.sp.? (E. 2291)	1	1	1	—	—	—	3	—
<i>Xylopia</i> sp.? (E. 4049)	1	—	—	—	—	—	—	—
31 species	268	146	51	9	11	63	548	83

\* Best regarded as a shrub.

- (b) Shrub layer
- Well-marked layer of shrubs and small trees to 5 m. (16 ft.). Undershrub layer to 2 m. (6 ft.) merging but distinguishable.
- Argemodendron macrophylla* Pax (E. 1563) v.f.-a.  
*Belonophora glomerata* M. B. Moss o.  
*Capparis afzelii* Pax o.  
*Lepidodermis lauriflora* Benth. v.f.  
*Memecylon jasminoides* Gilg (E. 1984) r.  
*Microdesmis zenkeri* Pax o.  
*Rinorea ardisiaeflora* O. Ktze. a. (immature)  
*R. poggei* Engl. a. (dominant)  
*Tapura fischeri* Engl. o.  
*Thecacoris lucida* Hutch. (E. 1616) r.  
*Whitfieldia elongata* C.R.Cl. (E. 1552) a.
- (c) Herbs
- (i) Dicotyledons:
- Achyranthes aspera* Linn. (E. 2286) o.  
*Brachystephanus* sp. (E.sn.) o.  
*Brilliantaisia* sp. (E.sn.) o.  
*Cyathula prostrata* Bl. (E. 5113) f.-a.  
*Dialypora* sp. (E.sn.) o.  
*Geophila uniflora* Hiern (E. 433) f.  
*Justicia glabra* Roxb. (E. 943) o. (openings)  
*Lankasteria elegans* T. Anders. (E.sn.) o.  
*Mellera lobulata* S. Moore (E. 1476) o. (openings)  
*Monothecium glandulosum* Hochst. (E. 3333) f.  
*Phyllopsis* sp. (E. 2308) o.  
*Pseudanthemum ludovicianum* Lindau (E.sn.) o.  
*P. tunicatum* Milne-Redhead (E. 2273) o.-f.
- (ii) Monocotyledons:
- Aframomum* sp. (E.sn.) o.  
*Burfordia* n.sp.? (E. 1414) o. (v.f. openings)  
*Calanthe corymbosa* Lindl. (E. 2106) r.  
*Commelina* sp. (E.sn.) o.  
*Corymbis velutiuschii* Rehb. f. (E. 3396) f.-v.f.  
*Lepidaspis cochleata* Thwaites (E. 3329) v.f.-a. (locally dominant)  
*Olyra latifolia* Linn. (E. 1413) o.  
*Opismenus hirtellus* Beauv. (E. 2287) f.  
*Polia condensata* C.B.Cl. (E.sn.) o.-f.  
*Streptogynis gerontogaea* Hook. f. (E. 5179) o.
- (iii) Ferns:
- Asplenium macrophlebium* Baker (E. 2098 A) o. } on rotting logs  
*Asplenium* sp. o.  
*Doryopteris concolor* Kuhn (E. 2026) o.  
*Doryopteris* sp. o.  
*Pteris tripartita* Sw. (E. 1469) o.
- (d) Climbers

No small climbers except in gaps. One plant of *Vanilla imperialis* Kraenzl. (E. 2062). At least thirty-one high-climbing lianas, all but two very large and at least as thick as a man's wrist. Many species involved but only the following identified:

- Alafia* sp. (E.sn.)  
*Clerodendron kentrocaule* Baker (E. 2207)  
*Entada phaeocoloides* Merr. (E.sn.)  
*Hippocratea* spp. (two)  
*Pisonia aculeata* Linn. (E.sn.)  
*Strychnos aculeata* Solerod. (E. 3817)  
*Strychnos* sp.
- (e) Epiphytes
- A few large *Alstonia* and *Cynometra* smothered with epiphytic ferns and orchids but this is not the general rule though most large trees bear some.
- Aerangis calantha* Schltr. (E. 5461)  
*Ancistrorhynchus ovatus* Summerhayes (E. 3360)  
*Angraecum infundibulare* Lindl. (E. 2040)  
*Arthropteris orientalis* Posth. (E. 2043)  
*Asplenium africanum* Desv. (E. 2109)  
*Bolustella imbricata* Schltr. (E. 2245)  
*Bulbophyllum cupuligerum* Kraenzl. (E. 2059)  
*Calyptrochilum christyanum* Summerhayes (E. 2054)  
*Chamaejasme vesicata* Schltr. (E. 2103)  
*Cissus* sp. (growing from *Platygyrium* tuft)  
*Cyclophorus meckonii* Hieron. (E. 2117)  
*Cyrtorhis* ?sp. nov. (E. 5449)  
*Diaphanandhe bidens* Schltr. (E. 5191)  
*D. fragrantissima* Schltr. (E. 2228)  
*Drynaria laurentii* Hieron. (E. 2042)  
*Encrinidion macrophyllum* Summerhayes (E. 5213)  
*Ficus depauperata* Sim  
*F. stipulifera* Hutch.  
*Menispermaceae* (inlet.)—growing from *Platygyrium* tuft  
*Oberonia disticha* Schltr. (E. 5212)  
*Peperomia* sp. near *P. ruenzoricensis* Rendle (E. 2093)  
*Platygyrium angolense* Wely. (E. 5478)  
*Podanigis aactyloceras* Schltr. (E. 2242)  
*Polypodium phymatodes* Linn. (E.sn.)  
*Polytachya paniculata* Rolfe (E. 2175)  
*P. polychaete* Kraenzl. (E. 2186)  
*P. stuhlmannii* Kraenzl. (E. 1411)  
*Polytachya* sp. (E. 5465)  
*Rangiers muscicola* Summerhayes (E. 3395)  
*Rhipidoglossum rutulum* Schltr. (E. 2256)  
*R. xanthopollinium* Schltr. (E. 4047)  
*Rhipsalis cassipha* Gaertn. (E. 2171)  
*Sarcostemma viminalis* R.Br. (E. 179)  
*Tridactyle* sp. near *T. fibriata* Schltr. (E. 5459)  
E. 5464 (Orchidaceae, probably new genus)
- (f) Parasites
- None
- (g) Timber regeneration

Abundant regeneration of *Cynometra* (all stages except very small saplings). No regeneration of any other canopy tree. Dense seedling regeneration of *Lastodiscus*.

Table 18. Sample Plot 9. Ironwood Forest

Species	(a) Trees 10 cm. (4 in.) diameter and over						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	Diameter class							
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Capparis afzelii</i> Pax	6	1	—	—	—	—	7	—
<i>Celtis soyauxii</i> Engl.	40	19	4	1	2	4	70	7
<i>C. zenkeri</i> Engl.	—	3	2	2	1	4	12	7
<i>Cynometra alexandri</i> C. H. Wright	21	13	7	6	6	71	124	83
<i>Funtumia elastica</i> Stapf (in gap)	1	—	—	—	—	—	1	—
<i>Holoptella grandis</i> Mildbr.	—	—	—	—	—	—	1	—
<i>Lasiodiscus mildbraedii</i> Engl.	261	40	1	—	—	1	302	1
<i>Mildbraediodendron excelsum</i> Harms	—	—	—	—	—	—	—	—
<i>Rinorea ardisiaeflora</i> O. Ktze.	48	5	—	—	—	—	53	1
<i>Strychnos</i> sp. (E. 1253)	3	2	1	2	1	7	16	10
<i>Tapura fischeri</i> Engl.	3	—	3	—	—	—	6	—
11 species	383	83	18	11	10	88	593	109

(ii) Monocotyledons:

*Aframomum* sp. (E.sn.)

*Anchomanes* sp. (E.sn.)

*Bufoerestia* n.sp.? (E. 1414)

*Opismenus hirtellus* Beauv. (E. 2287)

*Olyra latifolia* Linn. (E. 1413)

(b) Shrub layer

Considerable breakage by elephants. Many young *Lasiodiscus mildbraedii* and *Rinorea ardisiaeflora* intermixed with the following shrubs and small trees:

*Acalypha* spp.

*Argemuellera macrophylla* Pax (E. 1563)

*Randia urecliformis* Hiern

*Thecacoris lucida* Hutch. (E. 1616)

*Whitfieldia elongata* C.B.Cl. (E. 1552)

(c) Herbs

*Polyspatha paniculata* Benth. (E.sn.)

*Streptogyne gerontogaea* Hook. f. (E. 5179)

(iii) Ferns:

*Asplenium protensum* Schrad. (E. 2025)

*Doryopteris concolor* Kuhn (E. 2026)

*Tectaria? fernandensis* C. Chr. (2064)

(d) Climbers

Herbaceous climbers absent except in openings. Lianas rare; four large and five small.

(e) Epiphytes

Epiphytic figs uncommon, only three noted (*Ficus depauperata* Sim, *F. polita* Vahl and *F. dawei* Hutch.). Epiphytic ferns and orchids few except on one or two large old trees (e.g. *Holoptella*, which bore many *Platygerium* tufts), including *Rhipidoglossum* spp. (two), *Polystachya* sp., *Calyptrorchilus christyanum* Summerhayes (E. 2054) and 2-3 species of ferns. No *Rhipsalis*.

(f) Parasites

None

(g) Timber regeneration

Many seedlings and small plants of *Cynometra*; and a few small saplings. Abundant seedling regeneration of *Lasiodiscus*.

(a) Trees 10 cm. (4 in.) diameter and over

Species	Diameter class						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Alstonia congenensis</i> Engl.	—	1	—	—	—	1	2	1
<i>Antiaris toxicaria</i> Lesch.	—	—	—	—	—	1	1	1
<i>Aphania senegalensis</i> Radlk.	—	1	—	—	—	1	2	1
<i>Balanocistrus davei</i> Stapf	40	1	—	—	—	—	1	1
<i>Capparis afzelii</i> Pax	17	7	—	—	—	—	41	—
<i>Celtis brownii</i> Rendle	11	7	2	—	—	—	26	—
<i>C. soyauxii</i> Engl.	4	5	1	—	—	—	19	—
<i>C. zenkeri</i> Engl.	—	1	4	3	—	1	17	4
<i>Chrysophyllum albidum</i> G. Don	—	—	—	1	—	—	3	1
<i>Chrysophyllum</i> n.sp.? (E. 2248)	—	—	—	1	—	—	1	1
<i>Cola cordifolia</i> R.Br.	—	—	—	—	—	—	1	1
<i>Cynometra alexandri</i> C. H. Wright	5	18	10	14	1	61	115	82
<i>Dialium</i> sp. (E. 3376)	1	—	—	—	—	—	1	1
<i>Drypetes ugandensis</i> Hutch. (E. 3078)	—	—	—	—	1	—	1	1
<i>Entandrophragma angolense</i> C.DC.	—	—	—	—	—	—	—	—
<i>E. utile</i> Sprague	—	1	—	—	—	1	1	—
<i>Ficus brachylepis</i> Welw. ex Hiern	—	—	—	—	—	—	—	—
<i>Lannea veluticarpa</i> Engl.	1	—	—	—	—	1	1	1
<i>Lepidolobus lauriflorus</i> Benth.	74	—	—	—	—	—	1	1
<i>Mimusops ugandensis</i> Stapf	—	—	—	—	—	—	—	—
<i>Rinorea ardisiaeflora</i> O. Ktze.	1	—	—	—	—	1	1	1
<i>Strychnos</i> sp. (E. 1253)	—	—	—	—	—	—	—	—
<i>Tapura fischeri</i> Engl.	26	2	1	—	—	—	29	—
<i>Tourraea floribunda</i> Hochst. (in gaps)	5	—	—	—	—	—	5	—
<i>Uvariopsis</i> n.sp.? (E. 2291)	3	—	—	—	—	—	3	—
25 species	189	44	19	19	9	69	349	97

## (b) Shrub layer

Layer composed chiefly of three species, all 2-4 m. (6-12 ft.) high, all equally abundant: *Rinorea poggei* (stems just under 10 cm. (4 in.) diam.; subwoody *Whitefieldia elongata* C.B.Cl. (E. 1552); and immature *Lepidolobus*. Bowed stems of *Capparis* with adventitious shoots form local thickets. Other shrubs and trees include:

<i>Argemuellera macrophylla</i> Pax (E. 1563)	f.
<i>Barleria brownii</i> S. Moore (E. 2304)	o.
<i>Landackeria schuriana</i> futhii Gilg (E. 2288)	f.
<i>Ochna</i> n.sp. (E. 2265)	o.
<i>Psychotria</i> sp. (E. 2321)	o.
<i>Tapura fischeri</i> Engl.	o.

## (i) Dicotyledons:

<i>Achyranthes aspera</i> Linn. (E. 2286)	f.
<i>Brilliantaisia</i> sp. (E. 2290)	l.a.-l.f.
<i>Girardinia condensata</i> Wedd. (E. 2281)	o.
<i>Halleria latifolia</i> H. Walt. (E. 1202)	f.
<i>Impatiens</i> sp. (E. sn.)	o.
<i>Phayloopsis</i> sp. (E. 2308)	o.

## (ii) Monocotyledons:

<i>Calanthe corymbosa</i> Lindl. (E. 2106)	o.
<i>Chlorophyllum</i> sp. (E. sn.)	l.f.

## (iii) Ferns:

None.	
<i>Olyra latifolia</i> Linn. (E. 1413)	o.
<i>Opismenus hirtellus</i> Beauv. (E. 2287)	f.
<i>Oryza eichengeri</i> A. Peter (E. 4884)	r.
<i>Pseudochlaena polystachya</i> Stapf (E. 5458)	r.
<i>Streptogyne gerontogata</i> Hook. f. (E. 5179)	o.

Only five large lianas and one small: scarcity a feature.

## (c) Epiphytes

Epiphytic orchids rare, except on one or two large trees. Only three species noted (*Ethiropoglossum* sp.; *Polystachya* spp.). A few clumps of *Platycerium angolense* Welw. (E. 5478) and some of *Asplenium africanum* Desv. (E. 2109). A few epiphytic figs.

## (f) Parasites

One specimen of the hemi-parasite *Loranthus* sp. (E. 2051), on branches. Several groups of the root parasite *Thonningia ugandensis* Hensl. (E. 1178).

## (g) Timber regeneration

Profuse seedling regeneration of *Cynometra*, mostly 5-15 cm. (2-6 in.) high, a few small plants to 30 cm. (1 ft.). No regeneration of other large trees.



Table 20. Sample Plot 11. Swamp Forest

(a) Trees 10 cm. (4 in.) diameter and over

Species	Diameter class						Total no. of individuals 10 cm. (4 in.) diam. and over	Total no. of individuals 41 cm. (16 in.) diam. and over
	10-19 cm. (4-7 in.)	20-29 cm. (8-11 in.)	30-40 cm. (12-15 in.)	41-50 cm. (16-19 in.)	51-60 cm. (20-23 in.)	61 cm. and over (24 in. and over)		
<i>Albizia zygia</i> Macbride	—	—	—	—	1	3	1	1
<i>Alstonia congenensis</i> Engl.	1	—	—	2	—	—	6	5
<i>Aningeria altissima</i> Aubr. & Pellegrin	—	—	1	—	—	—	1	—
<i>Antidesma laciniatum</i> var. <i>membranaceum</i> Muell. Arg.	—	—	—	—	—	—	1	—
<i>Baphia vollenkii</i> Bak. f.	1	2	—	—	—	—	3	—
<i>Bombax reflexum</i> Sprague	1	—	—	—	—	1	2	1
<i>Bosqueia phoberos</i> Bail.	9	1	2	—	—	—	12	—
<i>Bridelia micrantha</i> Baill.	1	1	—	—	—	—	2	—
<i>Caloncoba schweinfurthii</i> Gilg	2	—	—	—	—	—	2	—
<i>Canarium altissimum</i> Hutch. & Dandy	—	—	—	—	—	1	1	1
<i>Cathartium altissimum</i> Hutch. & Dandy	1	—	—	—	—	—	1	—
<i>Celtis durandii</i> Engl. var. <i>ugandensis</i> Rendle	2	2	—	—	—	—	4	—
<i>C. soyauxii</i> Engl.	4	1	—	—	—	—	5	—
<i>C. zenkeri</i> Engl.	1	1	—	—	—	—	2	—
<i>Chaetacme microcarpa</i> Rendle	12	1	—	—	—	—	13	—
<i>Chrysophyllum albidum</i> G. Don	—	—	—	—	—	—	—	—
<i>Cleistanthus</i> sp. prob. <i>C. polystachyus</i> Hook. f. ex Planch. (E. 3081)	3	1	—	—	1	—	4	1
<i>Cleistanthus patens</i> Engl. & Diels	1	1	1	—	—	—	3	—
<i>Cola cordifolia</i> R. Br.	3	—	2	3	1	2	11	6
<i>Conopharyngia holstii</i> Stapf	1	—	—	—	—	—	1	—
<i>Craibia brownii</i> Dunn	—	—	1	—	—	—	1	—
<i>Croton macrostachys</i> Hochst. ex A. Rich.	2	1	—	1	—	—	4	1
<i>Cynometra alexandri</i> C. H. Wright	6	3	2	2	4	5	22	11
<i>Dichrostachys glomerata</i> Chiov.	1	—	—	—	—	—	1	—
<i>Ehretia cymosa</i> Thonn.	1	1	—	—	—	—	2	—
<i>Entandrophragma angolense</i> C.DC.	1	—	—	—	—	—	1	—
<i>Erythrina excelsa</i> Baker	4	1	—	1	—	3	9	4
<i>Erythrophloeum guineense</i> G. Don	—	—	—	—	—	1	1	—
<i>Euphorbia lake</i> Schweinf. ex Pax	6	1	—	—	—	—	7	1
<i>Fagara angolensis</i> Engl.	1	—	—	—	—	—	1	—
<i>Fagaropsis angolensis</i> Greenway	2	—	1	—	1	—	4	1
<i>Ficus capensis</i> Thunb.	1	—	—	—	—	—	1	—
<i>F. dawei</i> Hutch.	—	—	—	—	—	1	1	—
<i>F. deklakena</i> A. Rich.	—	—	—	—	—	1	1	—
<i>F. namadensis</i> Hutch.	—	—	—	—	—	1	1	—
<i>F. polita</i> Vahl	—	—	—	—	—	1	1	—
<i>Funtumia latifolia</i> Stapf ex Schltr.	15	16	16	4	—	1	52	5
<i>Glyphaea lateriflora</i> Hutch. & J. M. Dalz.	3	—	—	—	—	—	3	—
<i>Guarea cedrata</i> Pellegr.	—	1	—	—	—	—	1	—
<i>Holoptelea grandis</i> Mildbr.	—	—	—	—	—	1	1	—
<i>Kaya anthotheca</i> C.DC.	23	1	—	1	4	7	36	12
<i>Klainedoxa gabonensis</i> Pierre	—	—	—	—	—	1	1	—
<i>Lasiacis mildbraedii</i> Engl.	10	1	—	—	—	—	11	—
<i>Laternaria chrysoclamys</i> Mildbr. & Burret	1	—	—	—	—	—	1	—
<i>Lepidoturus latiflorus</i> Benth.	16	—	—	—	—	—	18	—
<i>Lepionychia multiflora</i> K. Schum.	1	—	—	—	—	—	1	—
<i>Lindackeria mildbraedii</i> Gilg	1	—	—	—	—	—	1	—
<i>Macaranga schweinfurthii</i> Pax	15	8	2	—	—	—	27	3
<i>Macropus emini</i> Engl.	1	—	1	1	1	—	4	—



# SOME ECOLOGICAL OBSERVATIONS ON A TROPICAL FOREST TYPE IN THE GOLD COAST

By A. FOGGIE

*(With five Figures in the Text)*

## I. INTRODUCTION

From September to December 1944 the writer was preparing a Working Plan for the Bobiri Forest Reserve in Ashanti (Gold Coast), and in February and March 1945 revisited it to prepare profile diagrams of one of the forest types. The following observations are based on this work. The preparation of the profile diagrams was part of a larger project initiated by Capt. R. C. Marshall, Chief Conservator of Forests, with a view to determining whether a clear distinction and definition of the rather indefinite 'types' accepted by the Forest Department Staff could be drawn. It is hoped that the full results of this project will be published eventually as a Departmental Bulletin, but owing to shortage of staff this is likely to be deferred for some years. The writer has therefore taken advantage of his leave to prepare these notes on the observations made in the type in which he worked for comparison with the descriptions of other tropical forest types of Davis & Richards (1933, 1934) and Richards (1936, 1939). The methods suggested by Richards, Tansley & Watt (1939) were followed as far as circumstances allowed.

## II. GENERAL DESCRIPTION OF THE AREA

The Bobiri Forest Reserve lies in Ashanti, 16 miles (25.8 km.) east of Kumasi between latitudes  $6^{\circ} 39'$  and  $6^{\circ} 44'$  N. and longitudes  $1^{\circ} 15'$  and  $1^{\circ} 23'$  W. In relation to the general topography of the country it lies south and east of the Koforidua-Mampong scarp which runs in a great arc from Koforidua in the south-east to Mampong and beyond in the north-west. The scarp varies in height along its length with peaks rising to 2700 ft. (820 m.). The scarp face is to the south-west with a more gentle slope to the Obosom and Afram plains and the Volta River in the north and east. It is the major topographical feature of the Gold Coast and also marks the major geological division in the country. At the present day south and west of the scarp the vegetation is that of the Closed Forest zone, and north and east of it Savannah Woodland is met within a short distance.

The Bobiri Reserve lies on gently undulating country between 600 ft. (183 m.) and 800 ft. (243 m.), about 15 miles (24.6 km.) south-west of the scarp. The general slope is from north-west to south-east, in which direction all the streams in the reserve flow. They are tributaries of the Anum River which flows southward just east of the Reserve and is itself a tributary of the River Pra which reaches the sea between Cape Coast and Sekondi. The Bobiri Reserve is 21 sq. miles in extent.

## III. GEOLOGY

According to the Geological Survey Map, 1934, the whole reserve is on rocks of the Cape Coast Granite Series. Rock outcrops or boulders are extremely rare however, and under the tropical conditions there has been deep weathering of the parent rock, and soil

formation processes have largely marked the parent material. The stream beds are usually of quartz gravel or a white sand. Occasionally boulders of ironstone occur, but these are of secondary formation, relics of a previous laterized soil from an earlier ground-level.

#### IV. SOILS

The soils of the Reserve have not been intensively studied. In general they form a catena. On the tops of the ridges they are Tropical Red Earths, occasionally showing the early stages of laterization by the presence of ironstone gravel. In texture they vary from sandy loams to clay loams. Descending the slopes of the ridges there is generally a narrow band of yellow to brown soil similar in texture to the Red Earth. This passes into a grey leached sandy or silty soil on the river flats. It may be covered with a thin layer of black peat; this does not appear to deepen however, nor to penetrate into the soil below.

There is no visible alteration of the vegetation structurally or floristically between the Red Earths of the tops and the Yellow and Brown Earths of the slopes, but the permanently moist soil of the valley bottoms carries a riverain vegetation. Only the dry-soil type of vegetation was studied in detail, and soil pits were dug and described by layers in each of the two plots studied. No samples were taken for analysis. The soil profile descriptions made in the field are given below:

In middle of Strip 1 (see Figs. 4, 5).

Litter 0.0–0.64 cm. Layer of leaves, lower partly decomposed.

Layer 1. 0.0–2.54 cm. Purplish grey with some humic material, light sandy silt, some tiny bleached particles, full of fibrous roots, dry.

Shading into:

Layer 2. 2.54–10.16 cm. Reddish brown, small cloddy loam (sand-silt-clay), small quartz gravel, occasional particles of red iron oxide just crushable by fingers, fibrous roots in fair quantity, just moist.

Passing at irregular depths into:

Layer 3. 10.16–28.4 cm. Abundant quartz gravel, shot to small pea size with some larger stones 2.5 × 1.3 cm. approx. in matrix of indurated brick red loam, some pebbles of ironstone, also particles of red iron oxide not yet fully hardened, roots occasional, moist.

At the base of this layer, about 25 cm., there appeared to be a slightly greater concentration of these particles than elsewhere.

This layer shaded into:

Layer 4. 25.4–96.52 cm. (bottom of pit). Quartz gravel and stones in brick red matrix of heavy loam to clay, red ironstone particles and small ironstone pebbles scattered throughout. Layer very uniform throughout its depth. Occasional roots pass through this layer to the bottom of the pit. Definitely moist to touch.

The drainage was considered in the field to be slow, but deep, and could not be classed as imperfect or impeded.

The profile was classed as a Tropical Red Earth.

In middle of Strip 2.

Litter 0.0–2.54 cm. Loose layer of leaf litter, structure visible.

Layer 1. 0–2.54 cm. Layer of dark purplish brown crumbly humic sandy loam, profuse rooting throughout, dry, small black ants present.

Fairly clear boundary to:

Layer 2. 2.54–17.78 cm. Light brown, firm, rather amorphous sandy soil with a small amount of clay present, just perceptible to the touch, no stones, roots fairly abundant, just moist. At the base of this layer humus material appeared in old root channels.

There was a clear division to:

Layer 3. 17.78–81.28 cm. (bottom of pit). Indurated reddish brown layer with ironstone pebbles, small shot size, fine quartz gravel and quartz stones (approx. 10 cm. square) sparsely but evenly distributed, cemented in a matrix of stiff fine light brown clay, cloddy when broken by pick. Where ironstone crushed in digging brick red colour appeared but general tone was reddish brown. Specks of manganese occasional to rare, roots present but sparse, tap root of a shrub passed through to bottom of pit, just moist (drier than layer 2 and did not appear to have been affected by the rain two days before), soil termites present in small numbers.

The drainage was considered to be imperfect. Though not so deeply coloured as the profile in Strip 1, the soil was also considered to be a Tropical Red Earth.

## V. CLIMATE

Through the courtesy of the Meteorological Office, Accra Airfield, a large amount of climatological data is available for the area in which the Bobiri Reserve lies. This is from standard meteorological stations near towns or villages; no data for the microclimate within the forest are available.

*Temperature.* Figures are available from the stations at Kumasi, 25.8 km. west, and Konongo, 16.1 km. east-south-east, of the Reserve and are given in Table 1. They show the

Table 1. *Temperature*

Month	Kumasi, 1939-44					Konongo, 1936-44				
	Dry bulb		Mean		Mean ½ max. and min.	Dry bulb	Mean		Mean ½ max. and min.	
	07.00 G.M.T.	14.00 G.M.T.	Max.	Min.			09.00 G.M.T.	Max.		Min.
	° C.	° C.	° C.	° C.	° C.	° C.	° C.	° C.		
Jan.	21.0	30.1	30.75	19.1	25.0	23.2	29.1	19.4	24.3	
Feb.	22.0	32.0	32.5	20.3	26.4	24.8	31.3	21.2	26.25	
Mar.	22.5	31.8	32.5	21.3	26.9	25.5	31.4	21.75	26.5	
Apr.	22.75	31.0	31.9	21.6	26.75	26.0	31.3	22.0	26.8	
May	22.75	29.75	30.9	21.7	26.3	25.6	30.5	22.0	26.25	
June	22.4	28.5	29.6	21.4	25.4	24.6	29.0	21.6	25.2	
July	21.6	26.75	27.9	20.75	24.3	23.5	27.3	21.0	24.1	
Aug.	21.3	26.4	27.4	20.2	23.75	23.0	26.7	21.0	23.7	
Sept.	21.75	27.8	28.6	21.0	24.8	23.6	28.0	21.5	24.7	
Oct.	22.1	29.25	29.6	21.1	25.3	24.4	29.1	21.7	25.3	
Nov.	22.4	29.6	30.3	21.2	25.7	24.6	29.75	21.4	25.4	
Dec.	21.4	29.8	30.5	20.1	25.2	24.1	29.3	20.9	25.1	
Annual average	22.0	29.4	30.3	20.9	25.4	24.4	29.4	21.4	25.2	

extraordinary steadiness of the temperature and the very narrow range. The highest mean maximum is 32.5° C. in February and March, the lowest mean minimum 19.1° C. in January, while the greatest mean diurnal range, 07.00–14.00 G.M.T., recorded in Kumasi is from 22.6 to 32.0° C. in February, and the general mean range is only 7.4° from 22.0 to 29.4° C. The annual mean is 25.4° C. at Kumasi and 25.2° C. at Konongo.

*Rainfall.* Figures are available for Kumasi, Ejisu (12.9 km. west), Effiduasi (16.1 km. north-west), Bekwai (33.8 km. south-west), Konongo and Juaso (24.2 km. east-south-east) of the part of the Reserve in which the profile studies were made. The records are given in Table 2 and show remarkable consistency in total amount, number of wet days and annual distribution. The average rainfall in the Reserve may be safely put at approximately 152 cm. per annum falling in 120 days with a dry season of 3 months, generally December, January and February, and with a lull in the heavy rains during August, though the number of rainy days in that month is still high.

The records of the lowest recorded rainfall at these stations were also received and the totals are shown at the foot of Table 2. Full annual records for these years were received, but, as in all cases the decrease was due to a general lessening in the rainfall throughout the year and not to a single prolonged drought period, they are not reproduced in full. These records show that the vegetation must be able to survive occasional years when the rainfall is only 70% of the average, approximately 102 cm. per annum.

Table 2. *Rainfall*

	Kumasi 1906-43		Ejisu 1926-31		Effiduasi 1927-43 (less 1938)		Bekwai 1915-43 (less 1938)		Konongo 1939-44		Juaso 1916-43 (less 1938)	
Month	cm.	No. of wet days	cm.	No. of wet days	cm.	No. of wet days	cm.	No. of wet days	cm.	No. of wet days	cm.	No. of wet days
Jan.	1.6	2	5.1	No record	2.6	2	2.0	2	3.4	3	2.2	3
Feb.	5.6	4	6.5		6.9	4	6.2	3	4.6	4	5.4	4
Mar.	13.6	10	18.0		12.9	9	14.6	11	12.7	11	15.9	11
Apr.	14.2	10	16.8		14.4	11	16.4	9	16.9	9	17.0	11
May	18.6	14	20.3		20.2	15	20.5	15	21.6	14	18.7	17
June	22.4	16	26.2		25.8	15	23.4	17	24.6	16	25.5	19
July	12.8	11	11.4		13.7	8	12.3	12	12.3	12	14.5	13
Aug.	7.3	16	5.4		7.0	13	6.7	14	6.7	13	8.6	17
Sept.	18.6	18	20.6		21.9	13	16.3	15	18.0	18	20.5	19
Oct.	20.2	18	23.0		23.0	16	20.1	14	20.0	17	21.4	25
Nov.	9.9	11	8.1		10.1	8	13.3	12	9.0	11	12.9	15
Dec.	3.2	3	1.9		3.1	3	5.6	4	5.6	4	4.2	5
Annual total	148.0	133	163.3		161.6	117	157.4	128	155.4	132	166.8	159
Lowest recorded	101.8	Year 1919	144.3	Year 1927	117.9	Year 1936	117.4	Year 1926	146.8	Year 1940	118.0	Year 1936

Table 3. *Relative humidity*

Month	Kumasi 1939-43		Konongo 1939-44
	At 07.00 G.M.T.	At 14.00 G.M.T.	At 09.00 G.M.T.
Jan.	95	55	88
Feb.	95	50	86
Mar.	96	58	84
Apr.	96	65	83
May	96	68	85
June	96	71	86
July	96	73	86
Aug.	96	75	87
Sept.	96	72	88
Oct.	96	68	87
Nov.	96	66	87
Dec.	97	59	87
Annual average	96	63	86

*Relative humidity.* Figures are available for Kumasi, for 07.00 and 14.00 G.M.T., and for Konongo at 09.00 G.M.T., and are given in Table 3. These show the extremely high relative humidity, especially in the mornings, and its constancy at 07.00 and 09.00 G.M.T. throughout the year. The records of the relative humidity at 14.00 G.M.T. for Kumasi are more interesting. There is a drop during the day from 95 to 50% during February, at the end of the dry season; from then on the midday relative humidity steadily increases to a maximum in August, though at this time there is a lull in the rains. August is generally cool and cloudy however, as can be seen in the temperature records and records of sunshine.

*A tropical forest type in the Gold Coast*

*Sunshine.* Records are available only for Kumasi for 1941-4, Table 4, but are interesting in the very low figures throughout and the strongly seasonal distribution. The sunniest period is not during the dry season when the harmattan may bring a misty grey sky, but at the break of the rains in April and May. The sky then grows steadily more cloudy till in August there is a surprising record of zero hours of full sun. The amount of cloud lessens till November is nearly as sunny as March. The dry season weather then returns.

Table 4. *Sunshine. Kumasi. Period 1941-4*

Month	Average daily duration in hours
Jan.	3.19
Feb.	3.68
Mar.	4.16
Apr.	4.58
May	3.05
June	1.75
July	1.17
Aug.	0.00
Sept.	2.49
Oct.	3.76
Nov.	3.95
Dec.	3.66
Annual average	3.04

Table 5. *Wind, frequency and speed. Kumasi. Period 1939-43*

07.00 hr. G.M.T.											
Mean no. of days											
Months	Calm	Windy	Wind direction								Seasons
			N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.	
Dec., Jan., Feb.	72.6	17.4	2.0	1.6	1.2	1.8	2.0	5.0	2.2	1.6	Dry season
Mar., Apr., May	72.8	19.2	0.2	1.4	0.4	4.6	2.8	6.2	2.6	1.0	Spring. Beginning of the rains. Tornadoes most frequent
June, July, Aug.	76.8	15.2	0.2	0.8	0.0	1.4	3.8	6.2	2.2	0.6	Early rains
Sept., Oct., Nov.	69.8	21.2	1.2	1.2	0.4	3.0	6.4	4.2	3.8	1.0	Late rains. Occasional tornadoes
Annual means	292	73	3.6	5.0	2.0	10.8	15.0	21.6	10.8	4.2	
Mean speeds		3 m.p.h. 4.8 km.p.h.									
14.00 hr. G.M.T.											
Mean no. of days											
Months	Calm	Windy	Wind direction								Seasons
			N.	N.E.	E.	S.E.	S.	S.W.	W.	N.W.	
Dec., Jan., Feb.	35	55	3.0	5.4	1.6	8.8	9.6	13.2	7.0	6.4	Dry season
Mar., Apr., May	40.8	51.2	0.8	2.8	1.4	7.6	15.0	17.0	4.2	2.4	Spring. Beginning of the rains. Tornadoes most frequent
June, July, Aug.	44.2	47.8	0.6	3.0	0.6	3.2	14.6	15.2	7.8	2.8	Early rains
Sept., Oct., Nov.	42.6	48.4	1.8	1.6	3.0	5.6	16.0	11.6	6.8	2.0	Late rains. Occasional tornadoes
Annual means	162.6	202.4	6.2	12.8	6.6	25.2	55.2	57.0	25.8	13.6	
Mean speeds		3 m.p.h. 4.8 km.p.h.									

*Wind.* Records are only available for Kumasi and are given in Table 5 for 07.00 and 14.00 G.M.T. This shows the calmness of the early mornings; this, with calm nights, is a noticeable feature of the tropics. The number of calm days at 14.00 G.M.T. is also noticeable.

As regards wind direction the preponderance of the prevailing south and south-west winds at low levels even in the dry season is surprising. The effect of the harmattan can just be seen in the diagrams below and in the following contracted table:

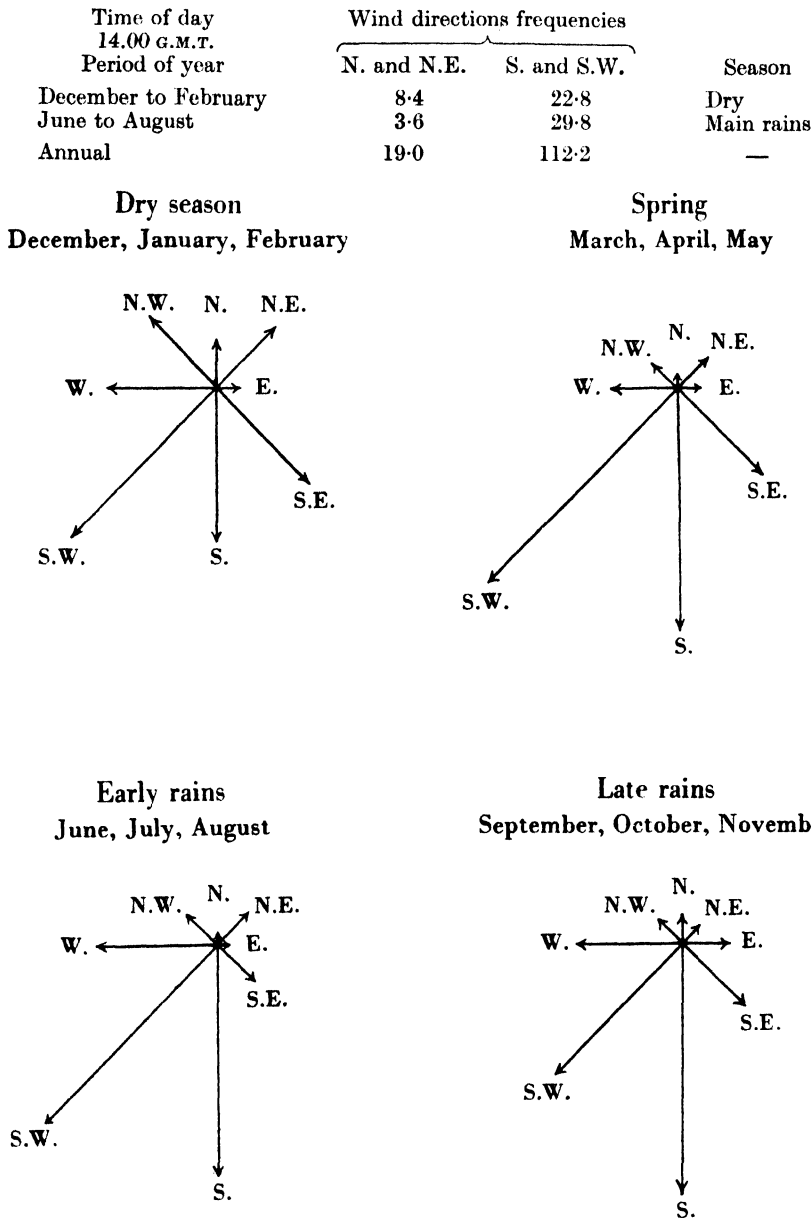


Fig. 1. Frequency of wind direction. Kumasi.

The harmattan by the time it reaches Kumasi is more a high-level drift than a surface wind. The mean wind speed is also very low: 3 m.p.h. (4.8 km.p.h.) with very little variation. Recording at 14.00 hr. largely omits the tornadoes and line squalls which usually rise later in the day, 16.00–20.00 hr., and only last a short period. The wind speed then rises quickly often up to 40 m.p.h. (65 km.p.h.) or more for very short periods. It is these storms which generally bring to earth the overmature dominants in the forest.

A climatological chart of Kumasi is attached (Fig. 2).



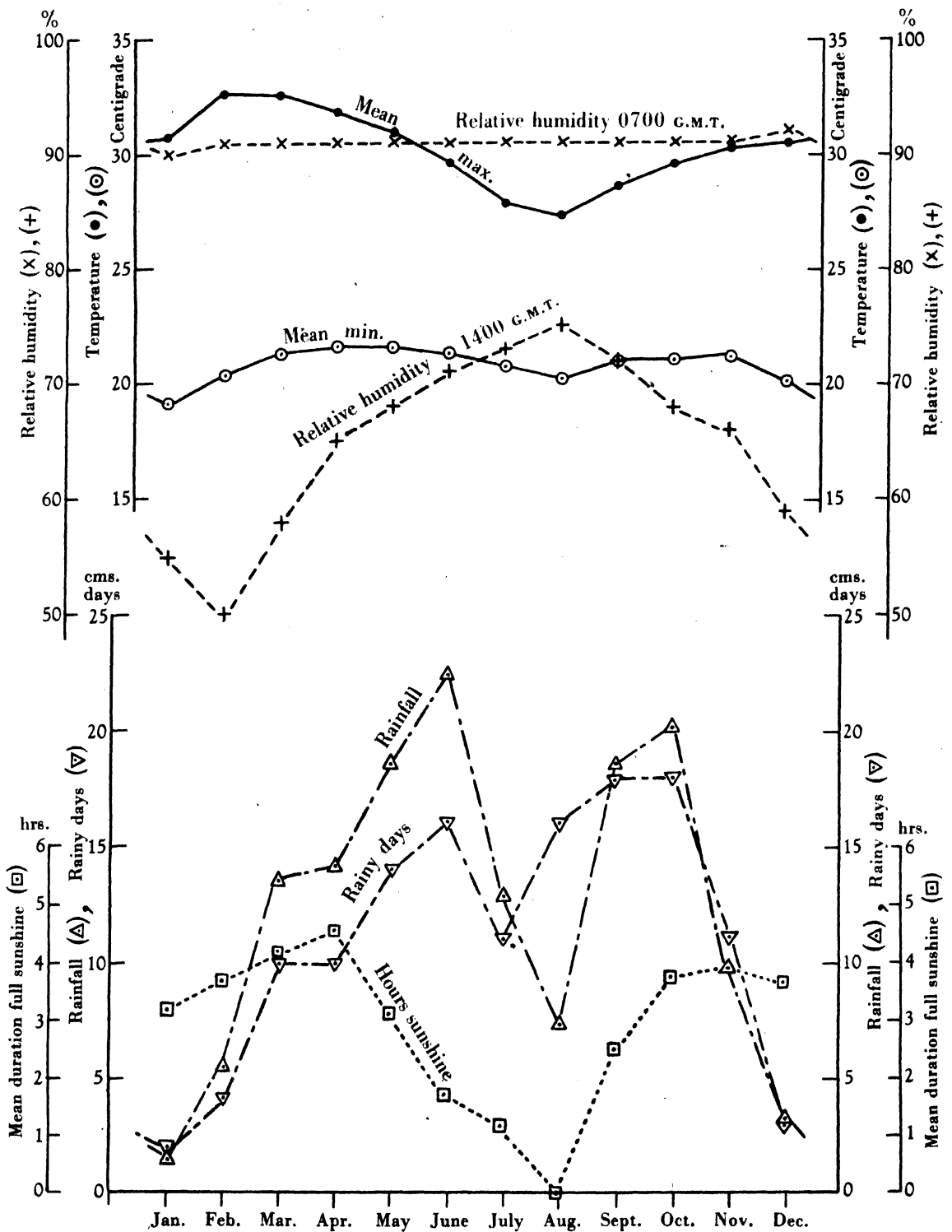
*A tropical forest type in the Gold Coast*

Fig. 2. Climatic chart. Kumasi.

Comparing these data with those given by Chipp (1927) it appears that he overestimated the occurrence of the harmattan as a surface wind, certainly within the closed forest zone. Its effect on the rainfall and relative humidity, however, as the monsoon dies away is striking. The humidity quoted in Chipp is that at 09.00 G.M.T. and this is not a very good indicator of the seasonal variation, as it is largely conditioned by the rise in temperature in the 2 hr. from dawn, at which time the air is practically saturated irrespective of season. The figures now given for the relative humidity at 14.00 G.M.T. at Kumasi show a distinct lowering in the dry season and a maximum in August.

It is not considered that the lull in the rains in August has any noticeable effect on the vegetation. The decrease is only in amount and not in the number of rainy days, it is comparatively cool and cloudy and the relative humidity is high.

## VI. HISTORY

The history of the area is of interest mainly in indicating whether the vegetation is primary or whether it has been previously affected by man, especially by farming. The seral stages of the recovery of the vegetation after farming, especially the later stages, are very imperfectly known, a decision based only on the observer's judgement is therefore liable to be at fault. The history and local records being all orally preserved must, however, also be considered with care, and, where the forester is concerned, local inquiry can rarely be trusted, as claims are then always put forward to ancient cultivation in the hope of preventing or frustrating reservation of the forest areas. The true status of the vegetation is therefore not known with any degree of certainty, and only a judgement based on both the local history and state of the existing vegetation can be given.

Historically it is known that Juaben the state or 'stool' in whose lands the greater part of the Reserve falls was a very powerful section of the Ashanti peoples until 1877 when an intertribal war took place resulting in the Omanhere of Juaben and many of his followers being expelled, where they set up the state of New Juaben in the Colony. There was probably some further migration during the Ashanti Wars. After peace was restored by the British occupation the population rose again and the introduction of cacao increased the area under cultivation.

Cultivation in the early days was purely subsistence food farming with a very long forest fallow. When Juaben was a powerful state presumably a considerable area of their stool lands were farmed, but owing to the lack of any relative figures for population it is impossible to say whether this was greater or less than at present. Whether the area now covered by the Bobiri Reserve was affected is not known. There are no old village sites within the area, but occasional specimens of the oil palm *Elaeis guineensis* Jacq. occur. This is often an indication of previous cultivation, but may be due to accidental dispersal or may indicate very old hunting camps. Such camps, a little hut in a clearing of under an acre with a few plantains and pawpaws and possibly a fruit tree, are widely distributed through all forest areas, but only affect the vegetation immediately adjacent to the clearing. Taking the area as a whole, the distribution by size classes of one or two species is rather curious, e.g. *Chlorophora excelsa* Bth. & Hook. f., *Entandrophragma utile* Sprague and *Terminalia ivorensis* A. Chev., which are well represented in the mature sizes, but very sparsely in the others, and would suggest an alteration in conditions. Here again lack of knowledge of the autecology of the trees, however, prevents any definite conclusion being drawn. It is known that the Bobiri area was not farmed subsequent to 1877 owing to a

ban placed on it by the Omanhere Kofi Serbus and, just before his death, the area was selected for reservation and finally reserved in 1937.

It may be said, therefore, that a large area of the Reserve is probably primary, and if areas have been farmed in the past this farming must have taken place 67 years ago or probably longer; at this stage the difference between primary and secondary forest is not detectable by inspection. The areas selected for intensive study of the structure are almost certainly primary.

Owing to the location there has been no felling for timber with the possible exception of an occasional *Chlorophora excelsa* Bth. & Hook. f. for local sawing.

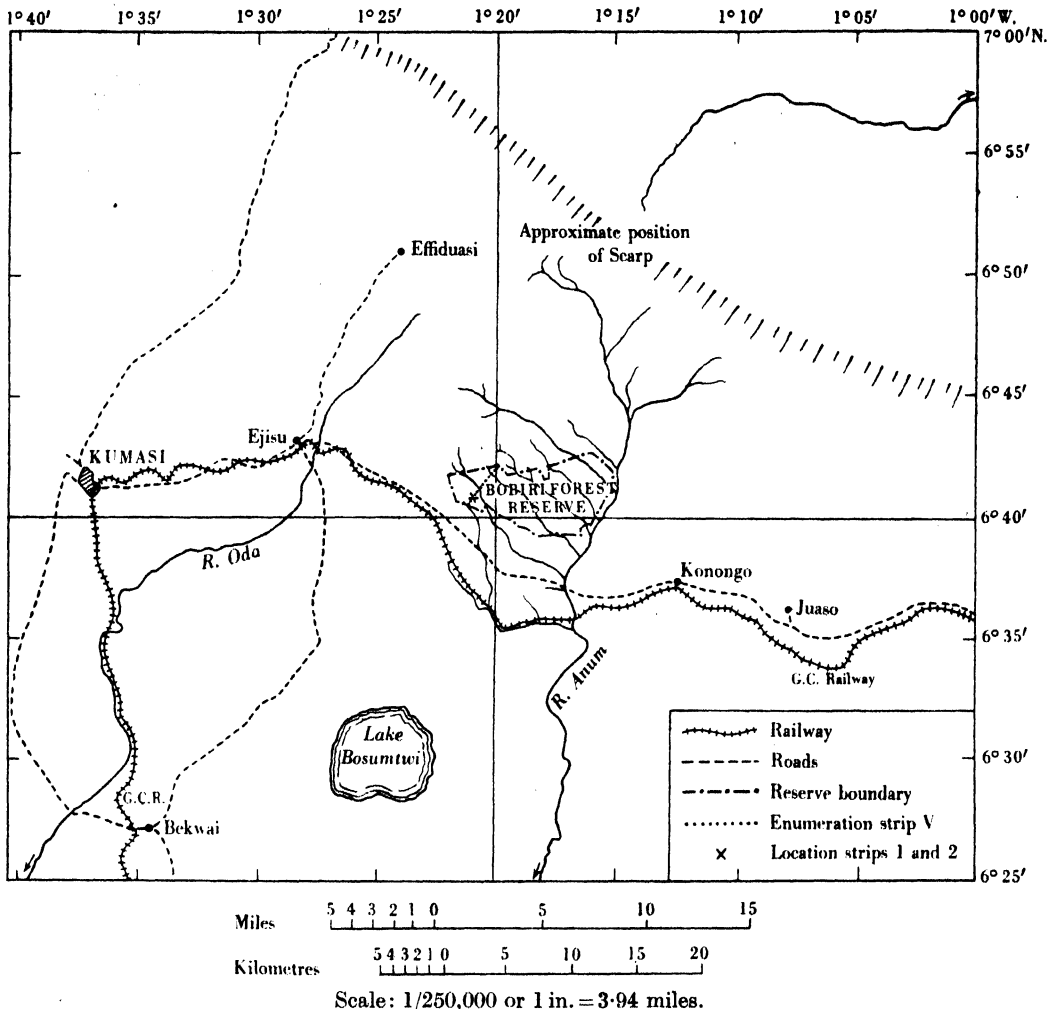


Fig. 3. Sketch-map of area round the Bobiri Forest Reserve.  
From sheet North B-30  
K G.C. Survey.

## VII. METHOD OF STUDY

After fairly extensive inspections within the Reserve it was decided that only two types of vegetation could be recognized: that occurring over by far the greater proportion of the area on the drier soils and that occurring in the river valleys, flats and swamps where the soil was permanently wet and periodically flooded or waterlogged.





Only the first type was studied in detail. It may be described as Tropical Lowland High Closed Forest, commonly known in West Africa as 'Mixed Deciduous' Forest (MacGregor, 1934).

The whole Reserve had been covered in 1939 by a 1% Enumeration Survey by strips 1 chain (20.1 m.) wide and 100 chains (2012 m.) apart run completely across the Reserve as nearly as possible at right angles to the main drainage. On these strips all trees of a foot (0.31 m.) girth and over were identified as far as possible and enumerated in 1 ft. (31 cm.) diameter (diameters mainly estimated by eye) classes. The 1939 Enumeration was checked over two strips by the writer and was found to be accurate for all valuable trees and the larger dominants. The species listed and their size class distribution on one of the strips checked are shown in Table 7. Though not a complete floristic list, it gives a fair idea of the common species in the emergent and dominant layers.

For the intensive study of the structure and composition two strips 200 × 25 ft. (61 × 7.6 m.) within the same strip (Enumeration Strip V) were selected. The first was 30 chains (603 m.), the second 40 chains (804 m.) within the forest from the southern boundary of the Reserve. They were selected as covering typical aspects of the structure, which is, however, very variable and could not be adequately covered in a single strip of these dimensions. They are on the top of a low, rounded rise between the headwaters of one stream and the valley of another, of approximately 700 ft. (215 m.) altitude.

Each strip was marked out by a narrow cleared line, while observations were made on the undisturbed herb layer. All shrubs or saplings of 15–17 ft. (4.6–5.2 m.) or less were cut, identified and recorded. It was found impossible to record the number of individual lianes. They were also found to be extremely difficult to identify, and the list given in Table 6 cannot be considered complete.

These shrubs and saplings formed the lower part of the closed canopy. They are not shown in the profile diagrams, and completely filled all gaps in the lowest canopy appearing in the profile. The lower level of their foliage was generally 8–10 ft. (2.45–3 m.) above the ground-level.

The position of all remaining trees was then plotted by offsetting and their girth at breast height (4 ft. 3 in. = 1.2 m.) was measured. All those which could be conveniently cut by cutlass were felled and identified and the following further measurements taken: height to tip, height to base of crown and to any distinctive fork, breadth of crown.

There then remained a number of larger trees on the strips which could not be felled in the time available, all dominants or emergents; these were measured standing, the total height and height to base of crown and/or fork being measured by an Abney level. The crown breadth was measured by directing a man holding a weighted pole vertically under the edges of the crown on either side and measuring between the points determined. This breadth was measured along the length of the strip as it appears in the profile.

All the standing trees were identified satisfactorily except two: 'Osubiri' and 'Dank-wakyrie' in the first strip. Only sterile material of both was available; the former belongs either to the genus *Uvaria* or to *Uvariopsis*, the latter could not be placed even in a family.

A full list of all plants noted on both plots is given in Table 6.

Table 6. List of all species recorded on sample strips. Area 0.229 acre (0.1 hectare)

Vernacular name (1)	Species (2)	Strip 1, 0.115 acre, 0.05 hectare				Strip 2, 0.115 acre, 0.05 hectare				Totals both strips	Remarks (19)
		Under 1 ft. girth				Under 1 ft. girth					
		A	B	C	D	A	B	C	D		
Efuobrodidwo	<i>Entandrophragma utile</i> Sprague	Seedlings	(3)	(4)	(5)	(6)	(7)	(8)	(9)	Over 9 ft. girth	Over 5 ft. girth
Penkwa	<i>E. cylindricum</i> Sprague				1				1		1
Wama	<i>Ricinodendron africanum</i> Müll. Arg.										1
Awabima	<i>Sterculia rhinopetala</i> K. Schum.	2							1		3
Eesakosua	<i>Celtis adolfi-frederici</i> Engl.				1				1		7
Wawa	<i>Triplochiton scleroxylon</i> K. Schum.										4
Mahogany	<i>Khaya ivorensis</i> A. Chev.				1						1
Dahoma	<i>Piptadenia africana</i> Hk. f.		1								7
Esepa	<i>Celtis soyauxii</i> Engl. 305 (314)										4
Eesakawkaw	<i>C. zenkeri</i> Engl.				5	1					1
Danta	<i>Cistanthra papaverifera</i> A. Chev.	4	1	1	1						7
Okure	<i>Bosqueia angolensis</i> Ficalho										1
Apapaye	<i>Guarea cedrata</i> (A. Chev.) Pellegrin 326	7	1	1	1						2
Yaya	<i>Amphimas pterocarpoides</i> Harms	1	1	1							6
Duabaha	<i>Hexalobus crispiflorus</i> A. Rich (288)				2	1					18
Dankwakylie	<i>Annonacea</i> nr. <i>Uvaria</i> or <i>Uvariopsis</i> (275)				2						2
Osubiri	Not identified 310		5	2	1						10
Okro	<i>Albizia zygia</i> Macbride										1
Awiafoesmina	<i>A. ferruginea</i> Benth.										1
Asamfona	<i>Chrysophyllum</i> sp.	4									11
Kokroboba	<i>Panda oleosa</i> Pierre (289)					1					3
Tenuro (Tendru)	<i>Tricheilia heudelotii</i> Planch (323)										2
Bamai	<i>Milletia rhodantha</i> Baill. (277)										1
Dwunkobiri	<i>Raphia pubescens</i> Hook. f. (292)				1	2					3
Samanta	<i>Busea occidentalis</i> Hutch ex Chipp (287)		7								8
Funtum	<i>Funtumia elastica</i> Stapf										3
Susmasa	<i>Neoboldia laevis</i> Seem.										1
Mamang	<i>Cassipourea</i> sp. 276		1								1
Afuna	<i>Strombosia pustulata</i> Oliv. (formerly <i>E. macrophyllum</i> A. Chev.)		2								4
Tiama-tiama	<i>Entandrophragma angolense</i> (Welw.) C.DC. var.		2								2
Wonton	<i>macrophyllum</i> Harms										1
Akyi	<i>Morus mesozygia</i> Stapf										5
Prono	<i>Blighia sapida</i> Koenig	4									2
	<i>Mansonia altiissima</i> A. Chev.	1									

Trees normally becoming dominant and emergent represented in these plots only by poles, saplings and seedlings in the understorey or herb layer

Trees normally becoming dominant and emergent represented in these plots only by poles, saplings and seedlings in the understorey or herb layer

Known to become emergent

Occasional emergent

[illegible]



Table 6 (continued)

*List of herbs noted*

Vernacular name (1)	Scientific name (2)	Strip 1 (3)	Strip 2 (4)	Remarks (5)
None known	<i>Leftaspis cochleata</i> Thw. 298	Present	Present	Frequency a.
'Ground Ivy'	Probably Commelinaceae 299	Present	Present	a.
None known	<i>Pteris ?atrovirens</i> Willd. 295, 307	Present	Present	f.
None known	<i>Bolbitis auriculata</i> (Sw.) Alston 309	Not noted	Present	f.
Sibiri	<i>Marantachloa flexuosa</i> Hutch. 319	Present	Not noted	f.
Tohorotohoro	<i>Sphenocentrum jollyanum</i> Pierre (294)	Present	Not noted	Occ.
None known	<i>Dracaena surculosa</i> Lindl. 297	Not noted	Present	Occ.

*List of lianes, climbers, scramblers and epiphytes*

Mutuo	<i>Prevostea africana</i> Bth. (300)	Present	Present	a. Seedlings abundant
Sahoma	<i>Millettia</i> sp. ? <i>barteri</i> Dunn or <i>hirsuta</i> (Dunn 302, 309)	Present	Present	a.
Mamfohan	<i>Strophanthus</i> sp. (? <i>hispidus</i> )	Present	Present	a.
Hwirem	<i>Culcasia angolensis</i> Welw. (306)	Present	Present	a.
Meye or Enuye	<i>Stenochlaema</i> sp. ? <i>sorbifolia</i> G. Sm. 296	Present	Present	a.
Duabrodidwo	Not identified	Present	Present	f.
Hühü	<i>Manniophyton africanum</i> Müll. Arg. (301)	Present	Not noted	Occ.
Babadua	<i>Tachyphrinium</i> sp. ? <i>violaceum</i> Radlk. 327	Not noted	Present	Occ. Strong colony in Strip 2
None known	<i>Alafia</i> sp. ? <i>barteri</i> Oliv. (325)	Not noted	Present	Occ.
Oyie	<i>Calamus</i> sp.	Not noted	Present	Occ.
Mfia	<i>Ancistrophyllum</i> sp.	Not noted	Present	Occ.
Hamatwinabeng	Not identified	Not noted	Present	Occ.
Omensu	Not identified	Present	Not noted	Occ.
Nwire	<i>Acacia pennata</i> Willd.	Present	Not noted	Rare

An orchidaceous epiphyte on a broken branch also seen on Strip 2.

*Notes on the identification of species listed in Table 6*

The majority of the tree species were identified in the field. Some were identified through native names but as far as possible these were checked by inspection of characters in the field. In cases of doubt and where the species was not known specimens were taken. These were nearly all sterile, very few plants being found in flower or fruit at the time of observation, but they were taken to the Forest Department Herbarium and there matched with specimens whose duplicates had been named either at the Imperial Forestry Institute or Kew. As the specimens were mainly sterile and the storage space in the Forest Department Herbarium is severely limited and publication was not contemplated at the time, after matching most specimens were destroyed.

Species of which material was collected but later destroyed are shown by the writers collecting number, Gold Coast series, in brackets after the name. Species of which the specimens were retained in the Forest Herbarium are shown by the number unbracketed.

Thanks to the work of Mr Chidlow Vigne, S.A.C.F., the Forest Department Herbarium is extremely representative and very few specimens could not be matched. The specimen of *Tachyphrinium* was one and it was identified through the Flora of West Tropical Africa, but only so far as to place it as probably *T. violaceum* Radlk.

Where species are shown as questionable or incompletely named but the specimen destroyed, the match could not be considered perfect lacking flowers or fruit as the specimen was sterile. An exception is *Chytranthus* sp. which was matched against a specimen not yet fully identified by the Imperial Forestry Institute.

## VIII. DESCRIPTION OF VEGETATION. DRY SOIL TYPE

The forest was composed of three strata. The first was a very open layer of emergents exceeding 120 ft. (37.2 m.) in height with exceptional individuals reaching 200 ft. (61 m.). The tallest tree occurring on the strips was the *Triplochiton scleroxylon* K. Schum. of 163 ft. (50.5 m.), but many larger trees have been observed by the writer in his inspections.

Table 7. Table showing the valuable and common dominants and other common species with their size class distribution and numbers of trees present on a transect (Enumeration Strip V), one chain (20.12 m.) broad and 213.6 chains (4296 m.) long across the Bobiri Forest Reserve from south-west to north-east. Area 21.36 acres (8.64 hectares)

Species (1)	Girth classes					Total no. (7)
	1-3 ft. 0.31-0.92 m.	3-5 ft. 0.92-1.53 m.	5-7 ft. 1.53-2.13 m.	7-9 ft. 2.13-2.74 m.	Exceeding 9 ft. (2.74 m.)	
	(2)	(3)	(4)	(5)	(6)	
Becoming emergents and dominants						
<i>Triplochiton scleroxylon</i> K. Schum.	32	16	18	9	15	90
<i>Entandrophragma cylindricum</i> Sprague	18	2	0	2	9	31
<i>E. angolense</i> (Welw.) C. DC. var. <i>macrophyllum</i> Harms	68	8	4	0	0	80
<i>E. utile</i> Sprague	1	0	0	1	3	5
<i>Entandrophragma</i> spp.	15	—	—	—	—	15
<i>Khaya ivorensis</i> A. Chev.	30	3	0	0	3	36
<i>Ricinodendron africanum</i> Müll. Arg.	25	5	4	6	4	44
<i>Piptadenia africana</i> Hk. f.	31	4	2	3	1	41
<i>Antiaris africana</i> Hk. f.	32	5	2	0	1	40
<i>Terminalia superba</i> Engl. & Diels	9	1	2	7	5	24
<i>T. ivorensis</i> A. Chev.	2	1	1	0	1	5
<i>Cylicodiscus gabunensis</i> Harms	10	2	0	0	2	14
<i>Combretodendron africanum</i> Exell	4	7	0	2	0	13
<i>Chlorophora excelsa</i> Bth. & Hk. f.	3	0	0	0	1	4
<i>Mimusops heckelii</i> Hutch. & Dalz.	0	0	1	0	1	2
<i>Sarcocephalus didirichii</i> De Wild.	3	0	0	0	0	3
<i>Pterygota macrocarpa</i> K. Schum.			Not classified			4
<i>Cola ? cordifolia</i> R. Br.			"	"		4
<i>Alstonia congensis</i> Engl.			"	"		2
<i>Daniellia similis</i> Craib			"	"		1
<i>Ceiba pentandra</i> Gaertn.			"	"		?
Becoming dominants and subdominants						
<i>Celtis</i> spp. ( <i>C. soyauxii</i> Engl., <i>C. adolfi-frederici</i> Engl., <i>C. zenkeri</i> Engl. and <i>C. prantlii</i> Priemer, not separately booked)	667	40	16	10	3	736
<i>Sterculia rhinopetala</i> K. Schum.	103	20	12	2	0	137
<i>Chrysophyllum</i> spp.	73	4	2	0	1	80
<i>Cistanthera papaverifera</i> A. Chev.	56	10	3	0	—	69
<i>Bosquiea angolenses</i> Ficalho	37	13	2	0	—	52
<i>Guarea</i> sp.	38	3	1	0	—	42
<i>Mansonia altissima</i> A. Chev.	12	8	4	3	—	27
<i>Pycnanthus kombo</i> Warb.			Not classified			3
<i>Lannea acidissima</i> A. Chev.			"	"		3
<i>Xylia evansii</i> Hutch.			"	"		1
Lower story occasionally becoming subdominant						
<i>Bussia occidentalis</i> Hutch. ex Chipp	204	21	0	1	—	226
<i>Strombosia pustulata</i> Oliv.	96	8	0	0	—	104
<i>Corynanthes paniculata</i> Welw.	37	10	1	0	—	48
<i>Hymenostegia afzelii</i> Harms			Not classified			336
<i>Trichelia prieuriana</i> A. Juss.			"	"		191
<i>Rinorea oblongifolia</i> Marquand ex Chipp			"	"		114
<i>Baphia pubescens</i> Hk. f.			"	"		90
<i>Myrianthus</i> sp.			"	"		69
Others: including those not classified above, others only occasionally represented, and unidentified spp.	2493	205	64	14	13	2789
Totals	4099	396	139	60	63	4757
No. per acre	192	18.5	6.5	2.8	2.9	223
No. per hectare	474	45.7	16.1	6.9	7.2	551

Note on authority for specific names used in the text and in Table 7

These names are as cited in Hutchinson and Dalziel (1931-6) and the Draft Check List of the Gold Coast (Imperial Forestry Institute).

These emergents are irregularly spaced and often occur quite close together in groups. They are usually mature trees with rounded or flat crowns above a large fork. The majority are buttressed. Lianes may occur in their crowns and twine among their branches, the main stems of the lianes hang vertically like thick hawsers from the branches. The climber *Culcasia angolensis* Welw. may cover the trunks to the fork but rarely attains the upper crown. Epiphytes of the 'Birds Nest' type may occur on the branches and in the forks, but are not a regular occurrence; none was noted on the emergent trees in the two sample strips, but some were noted on emergents nearby.

Secondly, below the emergent stratum occurs a stratum which the writer considers can best be described as the Open Dominant Layer which extends from 30 ft. (9.3 m.) to 120 ft. (37.2 m.) above the ground. This is composed in part of occasional younger individuals of species which when mature will attain the emergent layer, but the greater part is composed of species whose height at maturity is normally under 120 ft. (37.2 m.). The majority are trees of 'good' form in the forestry sense, with small crowns and single straight stems. They may have thin plank buttresses or buttresses which do not project very far from the trunk at the base but extend up the trunk to considerable heights resulting in a fluted stem. The lower half of this deep stratum contains immature individuals of the emergent and dominant species, a few individuals of species more commonly occurring in the closed canopy and occasional short thick-boled, large-crowned trees such as the *Panda oleosa* Pierre and *Trichilia heudelotii* Planch. in the sample strips. Buttressing has not yet developed to any extent on the immature trees while the other trees in the lower half of this stratum are not buttressed.

Density is by no means uniform; there is again a noticeable tendency for trees to be grouped. Often if there is a single emergent such as the *Entandrophragma utile* Sprague or the *Ricinodendron africanum* Müll. Arg. on the first strip there will be a cluster of quite large trees growing closely round it often springing from between its buttresses and wholly under its crown. Or there may be a fairly close group of trees of like size, as for instance at the north end of the second sample strip.

This stratum does not form a closed canopy. The emergents and the open dominant layer with their lianes was only estimated to give 40-50% of full cover after the lower canopy had been removed from the sample strips. The small narrow crowns of many of the trees were remarkable. Lianes and climbers are most prolific in this layer, a crown without one entwined in it is exceptional and in many it was difficult to identify the foliage of the tree from that of the lianes upon it. Some of the smaller trees, which are shown in the diagrams with small solid crowns on slender stems, appeared in the field as pillars of greenery from the creepers festooning them.

Thirdly, there is the lowest tree layer or understory forming a closed canopy. It is composed of small trees or tall shrubs 10 ft. (3.1 m.) to 30 ft. (9.3 m.) high with occasional saplings and poles of the upper strata. This is the only stratum in which there is a clear numerical dominant, in the case of the samples studied, *Cleidion gabonicum* Baill., but pending further examination this species cannot be considered diagnostic of the forest type as in other areas of the same formation type it may be replaced by *Rinorea* sp., *Hymenostegia afzelii* Harms or others.

These understory trees are commonly single-stemmed with large crowns forming a dense mass of foliage between 10 and 30 ft. above ground; they are not buttressed. The stilt-rooted *Myrianthus arboreus* P.B. occurs occasionally. Leafless stems of lianes and

climbers were present in abundance, but the foliated lianes in this canopy appeared to be mainly young individuals struggling up to the higher strata. An exception was the monocotyledonous scrambler identified as *Tachyphrinium* sp., probably *violaceum* Radlk., of which a colony occurred in the second strip. This pushed its way to the top of the understory and spread a heavy mat of foliage over the top.

Below the understory there is a herb layer or ground flora which varies very greatly in amount from place to place, depending on the amount of light reaching the ground. In the first strip the cover was very dense and even, estimated at over 90%, the direct sunlight reaching the ground being confined to sunflecks between the leaves. The ground covering was estimated at 90% leaf tiller or bare soil and only 10% plant cover. The plants were weak colonies of the grass *Leptaspis cochleata* Thw. and a plant termed by the writer for reference 'Ground Ivy' from its habit. There were also abundant seedlings of the climber *Prevostea africana* Bth., fairly numerous seedlings of other trees and occasional sub-shrubs and ferns. In the second strip, in part, the total canopy was also very dense and the ground flora was similar. At the northern end, however, more light reached the ground. This was an area where an old emergent must have existed at some previous time; its rotted stump was seen on the edge of the strip, though all the rest had disappeared. The canopy was here estimated at only 75% and the herb layer was much more vigorous covering 60%, leaving 40% covered only with leaf litter and bare earth. The composition of the herb layer was not noticeably more varied, however. The grass *Leptaspis* had become much more vigorous and dominated the layer. The ferns were more numerous and much larger. 'Ground Ivy' was also present but was dominated by the taller grass and ferns. Seedlings of *Triplochiton scleroxylon* K. Schum. from the seed year of 1942-3 were surviving here.

No ground mosses were noted, though moss occurred freely on broken branches and dead trunks lying on the ground.

No bulbous plants were seen, but as the observations were made in the latter part of the dry season, this does not imply complete absence, though in the writer's experience this type of forest has little seasonal periodicity in the ground flora and bulbous plants are very rare.

In all layers the predominant leaf (or leaflet) size was mesophyll (on Raunkiaer's leaf size classification). Compound leaves, mainly pinnate with some palmate, were common in the emergent and dominant strata, but simple leaves predominated in the understory. Drip-tips only occurred occasionally in the lower tree canopy.

The proportion of trees deciduous in habit was determined by a count of all trees in the emergent and dominant tree layers passed in the thirty chains from the edge of the reserve to the first study strip. The results were:

	%
Trees leafless on that date (9 Feb. 1945)	42
Trees in leaf, new or old but known to be deciduous	25
Evergreen or not markedly deciduous	33

The understory is wholly evergreen; young individuals of species, definitely deciduous when they attain the dominant and emergent strata, are evergreen in habit while in this layer.

The deciduous habit is here by no means so strong or definite as in deciduous trees of the temperate zone. The individual tree sheds all its leaves and remains leafless for a

period, but both the time at which the leaves are shed and the length of the leafless period are very variable within the species and do not appear to be greatly affected by the current weather. Some may lose their leaves while the rains are still heavy and flush again at the beginning or in the middle of the dry season, others retain their leaves till the latter part of the dry season and flush again after the rains have begun and there are all variations between these conditions. Trees of the same species may therefore be seen in all stages at the same time throughout the dry season.

#### IX. NOTE ON THE VEGETATION OF THE PERMANENTLY MOIST SITES

The forest type occurring on the permanently moist sites is distinguished by the presence of *Raphia* palms and a great increase in the canes (rattans) *Calamus* spp. and *Ancistrophyllum* spp. It is much less dense in appearance in the emergent and open dominant layers and the understory is generally low. As regards the floristic composition of the emergent and dominant trees there is surprisingly little difference from the dry type. *Cistanthera papaverifera* A. Chev. is absent, *Entandrophragma* spp. are rare and *Celtis* spp. are not so common; *Terminalia superba* Engl. & Diels. and *Ceiba pentandra* Gaertn. are more commonly met with. *Mitragyna stipulosa* O. Kuntze, which is a common constituent of this type elsewhere and is confined to it, is rare in the Bobiri. *Sarcocephalus diderrichii* De Wild. is replaced by *S. pobeguinii* Pobegu. Otherwise the dominants are common to both types.

#### X. COMMENTS

The above description has been confined to the forest type studied in the Bobiri Forest Reserve, but forest of the same physiognomic formation and similar floristic composition covers a very great area of the Gold Coast. It passes gradually, almost imperceptibly, into the 'Evergreen Forest', or 'Rain Forest' of Richards, in the south-west of the colony and into a drier type of forest to the north and east. The structure is indeed very close to that of the Rain Forest proper and it is doubtful if a purely structural difference could be drawn between them. There is a greater difference between it and the drier type which has only two strata. Floristically the type described is exceptionally rich and extremely mixed. Owing to the large numbers of unclassified species the Enumeration Survey cannot be used as an indication of the number of species met with throughout the forest but on the two strips studied in detail, whose area is only 0.1 hectare, no fewer than 75 species occur in the tree and shrub layers alone, and they belong to fifty-three genera in twenty-three families. Of the emergents and dominants only *Triplochiton scleroxylon* K. Schum. and the *Celtis* spp. constitute any appreciable proportion of the whole. In the understory *Cleidion gabonicum* Baill. is here dominant, but as mentioned above this is thought to be a local occurrence.

The species occurring here are common to almost all the forest of this formation in the Gold Coast. Many are also constituents of the Rain Forest, while others appear in the drier type. A smaller number occur in all three.

The proportions in which the different species are represented vary from place to place very greatly, though *Triplochiton scleroxylon* K. Schum. and *Celtis* spp. generally remain the most numerous. With a mixture of this degree, proportions that could be expected to remain reasonably stable over a wide area could only be determined by careful sampling on a large scale. Chipp's (1927) attempt to divide the Gold Coast Closed Forest into a 'climax association' and several 'preclimaxes' or 'Associations' by the relative abundance

of certain dominants as indicator species has not been found workable. His *Cynometra-Lophira* Association is the Rain Forest type and his *Lophira-Entandrophragma* may cover the wide ecotone between the Rain Forest and the 'Mixed Deciduous' forest. His other preclimaxes cover both the type described and the drier type to the north, but they have not been found to be identifiable in the field. Marshall in the introduction to 'Silvicultural Notes on Some Gold Coast Trees' (1945), has subdivided the Closed Forest zone into only two associations: the *Lophira* Association, which is Rain Forest, and the *Triplochiton-Celtis* Association, which covers the rest.

The forest type under consideration was formerly known as the 'Mixed Deciduous' type, but this name has recently fallen into disrepute as too indefinite. This term has been applied to all shades of the Closed Forest between the 'Evergreen' or Rain Forest proper and the Savannah Woodland but, as the figures for deciduousness given above show, it is descriptive.

Whether the type described can be subdivided into homogenous associations with a constant set of dominants in reasonably stable proportions, similar to associations as used in the Temperate zones, must await further intensive study. Richards (1945), considering the Primary Tropical Rain Forest, quotes Aubréville (1938) as believing that the mixed tropical forest is a collection of species of similar ecological requirements which occur in combinations fluctuating from place to place and also in time. Aubréville is here describing the *forêt dense* of the Ivory Coast which includes, not only the Rain Forest proper, but parts similar to the type here described. The evidence the writer has so far been able to collect tends to support Aubréville's conclusions. If correct they will set the forester an even greater problem than that created by the multiplicity of species, as he will be unable to assume that the natural regeneration following exploitation will be of like species to the crop exploited. Experiments on natural regeneration in the tropical forest in West Africa are now in progress.

This paper is on work done while serving with the Gold Coast Forest Department and is published with the permission of the Acting Chief Conservator of Forests.

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## A POPULAR MISCONCEPTION REGARDING HUMIDITY AND THE NEED FOR CLOSER LIAISON BETWEEN METEOROLOGISTS AND ECOLOGISTS\*

BY A. P. G. MICHELMORE

At school we are taught that the Gulf Stream greatly affects the climate of the British Isles. We learn that a considerable belt around the coast of a continent differs from the interior in having a more humid and equable climate than the latter. This effect of bodies of water on the neighbouring land is apparently not confined to the great oceans. It is commonly believed, for instance, that the areas of unusually heavy rainfall on the north-western side of Lake Victoria and at the north-east corner of Lake Nyasa are due to the presence of these lakes.

Some years ago an eminent South African, Prof. Schwartz, wrote a book about the Kalahari. In it he proposed a scheme for damming the Zambesi and diverting much of its water southwards into the great hollows of the waterless country of the so-called desert of the Kalahari. He had two objects. The first was to irrigate great areas of new land, on which to settle land-hungry farmers. The second, the one which interests us, was to save water which now runs down the Zambesi to waste in the Indian Ocean, and to spread it out over the land to evaporate directly and to be transpired by the growing crops, with the object of raising the humidity of the air and increasing the rainfall of the drought-stricken north-western parts of the Union of South Africa. Prof. Schwartz's scheme so captured public imagination in South Africa, that the Government sent a special expedition of meteorologists, engineers and agriculturalists to Ngamiland to report on it.

The belief in the effect of water in moistening the air of the country around is extended also to smaller lakes and even to small streams, ponds and marshes. In ecological literature one constantly finds reference to the humidity of the atmosphere in the hollows containing such bodies of water.

Preferences for certain humidity belts have been used by a number of research workers to explain certain movements of locusts. A few years ago I decided to take some measurements of temperature and humidity at Lake Rukwa in Tanganyika, in order to try to understand the behaviour of the Red Locust, which I was studying there. This lake is a large body of water, being about 85 miles long. The results surprised me greatly, as they seemed to be at variance with ideas which I understood to be generally accepted. I found that in the middle of the day in the dry season the air over the shallow flood water of the lake was certainly damper than inland, but the differences were very much less than I had expected. Even 200 or 300 yards out over the water the air was very far from saturated, and relative humidities of only 40 or 50% could be read. Coming inland there was a decrease in humidity, but this ceased at a very short distance inland. Sometimes even places where there was still wet mud left by the retreat of the flood showed as low a humidity as the completely dry and burnt up areas hundreds of yards inland.

\* Short paper prepared for the joint meeting of the British Ecological and Royal Meteorological Societies, which the writer was eventually unable to attend.



A gradient of temperature also existed, there being often a difference of 5–10° C. between the flooded and the inland localities. Here also the effect of the lake was very local, the cooler zone seldom stretching further in than about 100 yards and often much less.

The problem was further studied by working out the absolute humidities for each reading. It then became apparent that the fairly clear gradients in relative humidity, or in saturation deficiency, a value which was also worked out, were very largely due to the temperature gradient. Similar gradients of absolute humidity also existed, but they were much less marked or regular. In other words, the air near the lake did not really contain much more water vapour than that inland, but it only behaved as if damper because it was cooler.

Another series of measurements was made at different heights above the ground or above the surface of the water in various places without or with varying amounts of vegetation. It was found that there was usually a strong vertical gradient of temperature and of humidity, both over water and on dry land. During the heat of the day the air near the ground or the water was both hotter and damper than that higher up. There was often more difference between the absolute humidity of the air at ground-level and that 5 feet above it, than there was at 5 feet out over the lake flood and at the same level hundreds of yards inland.

Vegetation affected both temperature and humidity. Moderately dense grass raised the temperature of the bottom layer of air, while very dense grass shaded the ground and kept the lowest layer of air cooler but raised the temperature of the middle layers, which were exposed to the sun but sheltered from the wind. The absolute humidity of the lower layers was raised by the presence of grass. Near the surface of the water higher humidities were sometimes found in grassy areas at the edge of the flood than over open water further out.

A feature of ecological interest is that the humidity gradients sometimes differed according to whether they were worked out for relative humidity or for saturation deficiency. This applied particularly to the dry ground inland, where the gradients were not always as definite as over or near the flood and were disturbed from time to time by the turbulence of the air. For instance, in some of the sets of measurements at different heights at one place the air would be driest up above in terms of relative humidity but driest near the ground in terms of saturation deficiency. On another occasion the saturation deficiency would show a regular gradient of falling humidity from ground-level to a height of 5 or 6 feet, while the relative humidity would decrease up to a height of 2 or 3 feet but show a slight increase again at the higher levels.

This brings me to my first concrete suggestion, which is that ecologists interested in humidity measurements should calculate all the different elements of humidity for every measurement. An organism may react directly to the degree of wetness in the air, in which case its behaviour may be correlated with relative humidity, or it may be affected by the evaporative power, in which case the correlation will be rather with saturation deficiency. Absolute humidity, on the other hand is unlikely to have a direct effect on an organism, but without an understanding of its variation the ecologist is likely to misunderstand the ecoclimate which he is studying. For instance, we may imagine a place where there is by day a strong temperature gradient between a flooded and a dry part of the area, but where the gradient of absolute humidity is not very marked. At night the temperature gradient will probably be reversed, the air being warmer over the water than over the dry land.

In an extreme case the dominant effect of temperature might even make the relative humidity higher and the saturation deficiency lower over dry land than over water, or at least the difference might be much less than would have been suspected from day-time studies of these two elements alone, without determinations of absolute humidity.

It is evident that evaporated water vapour is diffused so quickly into the upper atmosphere, at least when there is any wind, that its effect on the ecoclimate is much smaller and more local than is commonly believed.

That the smallness of the outside area affected by evaporation from a given surface applies also to climate on a larger scale, is shown by the following quotations from the report of the Kalahari Commission (1926) already mentioned. After an estimate that the swampy area of open water, reed, grass, timber and soil watered by the Okavango and Zambesi rivers, and all actively engaged in passing up water into the atmosphere throughout the year, averages some 2600 square miles and extends to 7200 square miles in very wet years, the report continues as follows: 'Perhaps one of the most striking features of the region is that one can turn one's back on the swamps or rivers, march a distance of anything from a dozen up to a few hundred yards, and find oneself in typical dry mopane or sand veld, such as stretches away for scores of miles, a waterless country, except for a few pans. Coming from the latter area, there is nothing in the vegetation to mark the proximity to the rivers or swamps until one is almost on the water's edge, where large water-loving trees form a narrow border; indeed the visitor might well be marching almost within hailing distance of some of the rivers and never suspect their presence.' After noting that the air at the edge of the swamps in the dry season was only 10% nearer saturation than away from them, the report goes on to say, 'It is clear, then, that the moisture evaporated from the water and reed surfaces must ascend rapidly, otherwise the air would soon become saturated, as a short calculation will amply demonstrate. Whatever might happen in the upper air a mile or more in height, we are unable to state, but this much can be affirmed, that the air at ground-level on the borders of these swamps is *normally far from saturation point*.' The report continues by explaining that the rainfall of such an area is controlled by the movements of far greater masses of air than is commonly realized and really on a continental scale. Finally it remarks as follows: 'The influence of the existing huge water and swamp areas on the climate of Ngamiland is, so far as can be observed and inferred, wholly negligible.'

The fact that it should have been necessary for a government to send a special expedition to a distant and inaccessible area, only to enunciate major principles of meteorology like this, shows that such principles are not widely enough known. There are doubtless many meteorologists here to-day, to whom my remarks have been commonplace. On the other hand there is clearly room for closer liaison between meteorologists and ecologists. Speaking as an ecologist with special interest in Africa, I can say from experience that there is a definite need for a text-book setting out in simple terms the main principles of tropical meteorology. Without such guidance the mere biologist is liable to be led badly astray when trying to explain problems on a wide geographical scale. For instance, throughout southern and eastern Africa the heaviest rain falls on the higher ground, and particularly on slopes facing the coast. A biologist might be forgiven for taking such a widespread phenomenon to be a general principle, yet in the Congo basin one finds (Goedart, 1938) that in general the wettest area is the middle of the basin, while the rims are drier, including even the Crystal Mountains, which lie not far inland from the humid Gulf of

Guinea. Again, in the course of locust studies I became interested in the possible differences in climate between the centre of a rift valley and the sides close to the escarpment wall, which was the only part from which records were available. Enquiries from official meteorological circles produced a sympathetic answer but no prediction of what differences were to be expected.

Returning to meteorology on a smaller scale, an exposition by a meteorologist of the effects of minor features of topography and vegetation on the general climate would be of great use to ecologists. Referring to Uvarov's exhaustive survey of previous work on Insects and Climate (1931), I find that there is in fact a book in German by Geiger (1927) on these lines, but it is not well enough known, and one in our own language would certainly fulfil a want.

More general work on microclimates, the climates of small surfaces and holes, is also needed. At present the ecologist interested in such problems has to make his own measurements. He can easily get immersed in such a body of physical measurements and calculations, that the biological side of the work is neglected. In hydrobiology there is a special branch of the subject dealing with the physics and chemistry of water. A similar systematic study of the atmospheric environment of land animals is needed. To be useful it should be done over a wide range of environments and in different climates. It would be best done by such teams of workers as have shown their use so well during war-time. The best method would be to run a set of instruments under standard conditions at the same time as the microclimatic readings are made. In this way many microclimates can be studied merely by sample measurements, which can be related to the standard climate. Changes in microclimate hourly, daily, monthly and even yearly can then be foretold by reference to the changes in standard climate, without making very long series of readings in each microclimate individually. This method has been used in Africa by Kirkpatrick (1935) and myself (unpublished). Referring again to Uvarov's survey already mentioned (1931), I see that he himself made somewhat similar proposals 17 years ago. The need for such work has not grown less during this period.

#### SUMMARY

Observations in Africa show that the effect of evaporating bodies of water and swampy vegetation on the humidity and the general climate of the surrounding country is much smaller and more localized than is commonly believed, at least by those who are not trained meteorologists. There is a need amongst land biologists for a wider dissemination of knowledge of the main principles of meteorology and of ecoclimatic differences. In microclimatology the present haphazard study by biologists interested in special ecological problems should be replaced by a systematic study of the whole subject in different climates. In making humidity determinations for ecological purposes the absolute humidity, relative humidity and saturation deficiency should all be computed.

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# OBSERVATIONS ON THE SAND DUNES OF BARBADOS, BRITISH WEST INDIES

By E. G. B. GOODING, M.A.

(*With two Figures in the Text*)

## INTRODUCTION

The island of Barbados is small and very fully cultivated. By far the greater part of the original flora has been destroyed or changed beyond recognition by the hand of man, and, for this reason, perhaps, there has been little written about the botany of the island. Thus, although the following account of the plant life of the sand dunes of Barbados is chiefly concerned with their floristic aspect, and a great deal of work remains to be done to substantiate the rather tentative conclusions drawn, it is felt that these observations are worthy of record.

## SITUATION AND CLIMATE

Barbados is largely a coral island and has an area of only 166 square miles. It is situated in the Atlantic Ocean, 59° W. and 13° N., about 100 miles to the east of the main arc of the West Indian islands, and some 200 miles north of the mainland of South America. The climate is tropical and oceanic, with mean annual temperature 26° C., mean annual temperature range 10° C., mean day and night temperature difference 4–6° C., mean annual rainfall 160 cm., wet season July to December with about 115 cm. of rain, and dry season January to June with about 45 cm. of rain. The prevailing wind is the E.N.E. trade, and the mean wind velocity is 16·8 k.p.h.: the strongest winds are in the dry season. The sunshine figure is 69% of the possible number of hours.

It is important to note that the rise and fall of the tide is small, being only about 1 m.

## SCOPE AND METHODS OF INVESTIGATION

The observations forming the basis of this paper were made with a view to obtaining full lists of the flora of the dunes, comparing the populations of these areas, gaining some knowledge of the environment of these plants, of the factors which control and limit their spread, and of the manner of dune development in Barbados.

Three areas were selected for intensive study: these particular areas were chosen because they showed less interference by the hand of man than any other sand-dune region. All the areas were on the 'windward coast', viz. the easterly side of the island: they were situated at Belle Plaine, Chancery Lane and Silver Sands. Two other beaches, one near Enterprise and the other at Maxwell's, provided some relevant data.

Superficial examination showed that while the usual separation into 'white' and 'grey' dunes (Hardy, 1934) is useful in denoting the general appearance of the dune vegetation, further classification into three major vegetation zones can be made with little difficulty. These are:

(i) A *Pioneer zone* of low-growing plants, the most important of which are *Phloxerus vermicularis*, *Sporobolus virginicus* and *Euphorbia buxifolia*. This zone is nearest the sea and is followed by

(ii) The '*Ipomoea pes-caprae*' zone, a zone of predominantly low growth-form plants, dominated by *Ipomoea pes-caprae*, but often flanked on the seaward side by the shrub *Tournefortia gnaphalodes*: other shrubs occasionally occur. This zone in turn is followed by

(iii) The '*Coccoloba*' zone, an association chiefly of shrubs, dominated by the sea grape, *Coccoloba uvifera*. Fig. 1, a rough section of the Belle Plaine beach, shows the general relationship of these zones. The dividing line between white and grey dunes is generally towards the landward margin of the *Ipomoea pes-caprae* zone.

It is interesting to note that in other West Indian islands, where a comparable zonation is found, *Canavalia maritima* is the dominant plant of the zone which corresponds to the *Ipomoea* zone of Barbados. *Canavalia maritima* is not common in Barbados.

More intensive study included the making of line transects from the seaward to landward side of the dunes and frequency estimations over stretches 200 m. in length and the whole breadth of the zone in question.

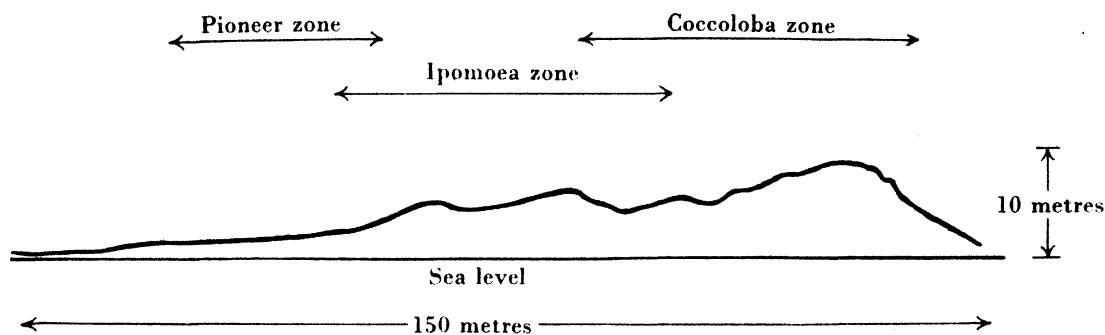


Fig 1. Rough section through sand dunes at Belle Plaine, from high-tide mark to rear of dunes.

Soil samples were taken at random within each zone. These were taken at a depth of 15 cm., as it was considered that the conditions obtaining at this depth would give a fair indication of the conditions which developing seedlings would have to survive. At the time that most of the soil samples were taken there had been about 3 cm. of rain during the previous 6 weeks. It was borne in mind that the chief establishment of seedlings would be in the wet season, but even then a wet day is usually followed by several dry days. Soil samples taken at Belle Plaine two days after a 7.5 cm. rainfall in August 1939 show figures little different from those of the dry season.

The soil samples were examined as follows:

(i) The water content was approximately determined by the oven method; 5 hours' heating at 100–105° C.

(ii) The salt content was determined by thoroughly washing 250 gm. of the dry soil with 500 ml. distilled water, evaporating this solution to about 25 ml. and titrating with *N*/20 silver nitrate solution, using potassium chromate as indicator.

(iii) The *pH* was approximately determined by B.D.H. comparator.

(iv) Humus was not determined quantitatively, but microscopic examination, and also shaking samples with water and noting the separation of humus, showed that humus content definitely increased with increasing distance from the sea.

The direction of wind currents was determined by lighting fires of dry wood at various points on the dunes and covering them with greener wood. The copious smoke so produced showed this clearly.

### DESCRIPTIONS OF THE AREAS

#### I. *Belle Plaine*

A strip of beach, about  $1\frac{1}{2}$  km. in length, facing east-north-east is backed by a line of dunes which is continuous except where it is cut by Long Pond and the alluvial flood-plain to the south of this stretch of water. The dunes have a maximum height of about 8 m., and an average breadth of about 100 m. The beach in front of the dunes is fairly wide, varying from 30 to 60 m. above high-tide mark.

Belle Plaine beach is situated in that part of Barbados which is not predominantly coralline, and the sand is very different in chemical constitution from that of the other localities considered, being siliceous and containing only 20–25% of calcium carbonate. The physical properties, however, of all three sands are, on the whole, similar.

The three vegetation zones are more or less distinct when taken over the whole area, but they tend to overlap considerably in some places, the accurate distinction between the *Ipomoea pes-caprae* zone and the *Coccoloba* zone being at times somewhat difficult.

1. *Pioneer zone*. This is the zone nearest the sea, and is extremely wind-blown and saline, chiefly from sea spray. The pioneer zone at Belle Plaine is only a few metres in width, and is situated at 30–60 m. from the high-tide mark.

(a) *Soil*. Samples of soil from this region show the following figures:

Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
50 m.	0.141*	9.4	8.5
	0.360*	3.5	
	0.280	5.0	
	0.313	4.0	
	0.211	4.4	
60 m.	0.250	3.8	8.5
	0.305	4.3	

\* Samples taken 2 days after a 7.5 cm. rainfall.

(b) *Floristic composition*. The only vegetation in this region is isolated patches of *Phloxerus vermicularis*, a prostrate plant around which blown sand is heaped up, and which often occupies the top of a small knoll bound together by its own dead parts, and very occasional individuals of *Sporobolus virginicus* or *Sesuvium portulacastrum*.

2. '*Ipomoea pes-caprae*' association. The embryonic dunes grade into the open association of the white dunes—an open phase of the *Ipomoea pes-caprae* association—which becomes more closed as distance from the sea increases. The *Ipomoea* zone has a width of from 25–100 m.

(a) *Soil*. Soil samples taken in this zone show the following figures:

Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
80 m.	0.350	2.20	8.0
100 m.	0.244	2.08	
	0.382*	1.96	
	0.820	1.34	
110 m.	1.250	2.00	8.0
	0.965*	1.23	
	0.680	1.52	

\* Samples taken 2 days after a 7.5 cm. rainfall.

(b) *Floristic composition*. All the plants of this association are of a low-growth form, except for a few poorly developed shrubs which occur occasionally in a few sheltered spots. The association is open in the early stages and in regions of shifting sand: in these regions *Sporobolus virginicus* is the most abundant plant. The long rhizomes of this plant bind the surface of the sand, and when covered by freshly blown sand they turn upwards and quickly grow to the new surface where they continue their growth and binding action. *Ipomoea pes-caprae* quickly follows *Sporobolus virginicus*, its long trailing stems also helping to check sand erosion and accumulating new wind-blown sand. The *Ipomoea* is also accompanied by *Euphorbia buxifolia* and, as the association becomes more closed, a number of other species appear. Of interest is the spasmodic appearance of *Canavalia maritima*, locally in great abundance, but with only a very limited distribution.

The frequency figures for four sample areas are as follows:

Low-growth forms	Growth form	Area				Frequency figure per 100
		I	II	III	IV	
<i>Canavalia maritima</i>	Ch	o. (lab.)	—	—	—	10
<i>Corchorus aestuans</i>	Th	v.r.	v.r.	—	—	5
<i>Euphorbia buxifolia</i>	Ch	f.	f.	f.	f.	60
<i>Ipomoea pes-caprae</i>	Ch	v.ab.	v.ab.	ab.	v.ab.	95
<i>Lippia reptans</i>	Ch	o.	—	—	—	10
<i>Pectis humifusa</i>	Ch	r.	r.	f.	—	25
<i>Philoxerus vermicularis</i>	Ch	r.	—	—	—	5
<i>Portulaca oleracea</i>	Ch	o.	r.	—	—	15
<i>Sporobolus virginicus</i>	H	v.ab.	v.ab.	ab.	v.ab.	95
<i>Stenotaphrum secundatum</i>	Ch	o.	f.	o.	—	35
Shrubs						
<i>Calotropis procera</i>	P	—	o. (lab.)	—	—	10
<i>Chrysobalanus icaco</i>	P	—	o. (lab.)	—	—	10
<i>Coccoloba uvifera</i>	P	—	o. (lab.)	—	—	10
<i>Tournefortia gnaphalodes</i>	P	—	f.	—	—	15

3. '*Coccoloba*' association. To the back of the *Ipomoea pes-caprae* association occurs a rather poor community of *Coccoloba uvifera*, of average width about 50 m.

(a) *Soil*. Soil samples show the following figures:

Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
130 m.	1.95	0.38	7.5
150 m.	2.08*	0.47	7.5
	1.34	0.24	
	1.52	0.46	
180 m.	1.83*	0.20	7.5
	1.96	0.33	

\* Samples taken 2 days after a 7.5 cm. rainfall.

The soil in these samples was considerably darker and richer in humus than that of the Pioneer and *Ipomoea* zones.

(b) *Floristic composition*. The boundary between the *Coccoloba* association and the *Ipomoea pes-caprae* association is very ill-defined. The *Coccoloba* association creeps forward into the *Ipomoea* association in sheltered spots, occupying the depressions behind the dunes, sometimes in quite advanced areas, while the *Ipomoea* association occupies the tops of the dunes. On the other hand, in wind-blown gaps between the *Coccoloba* supporting dunes the *Ipomoea* association is developed in a series of long, landward-reaching tongues. The vegetation of these areas changes considerably on the leeward side of the

dunes and eventually a very open scrub community, with *Croton flavens* as the most common shrub, is developed.

*Coccoloba uvifera* ultimately tends to form closed stands, often to the exclusion of all other species, but sometimes mixed with other shrubs.

The limiting effect of wind on the *Coccoloba* association is conspicuous. Behind most of the higher dunes in the *Ipomoea pes-caprae* association a few *Coccoloba* shrubs are to be seen, with their tops sharply limited as they reach the level of the protecting dune. Further back, on the higher dunes, *Coccoloba* often occupies the summits, but the seaward individuals are always extremely stunted and poorly developed: behind these the *Coccoloba* gradually increases in height. The same is true of the other shrubs of this association.

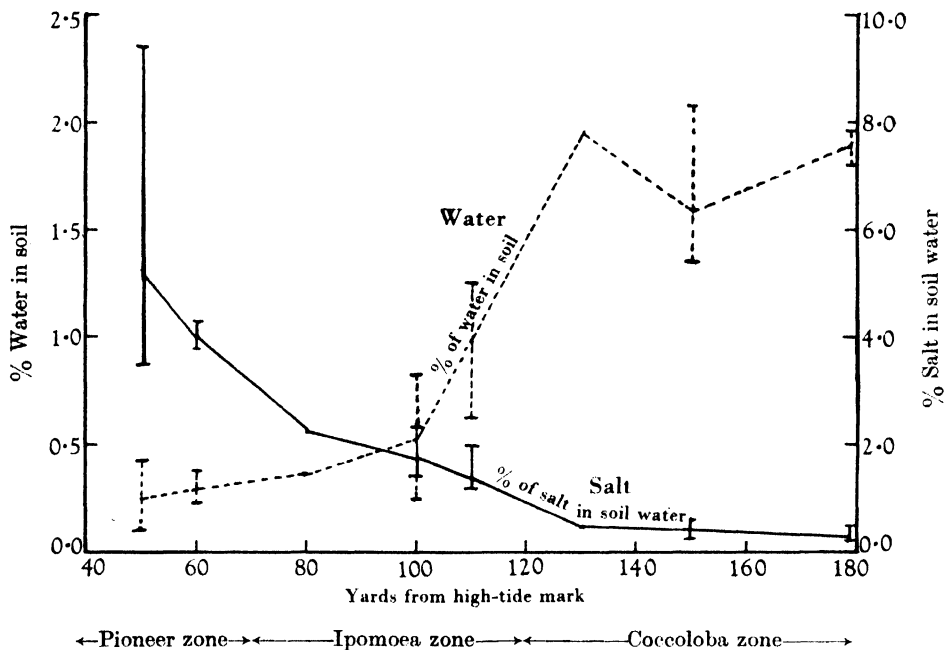


Fig 2. Diagram showing percentages of salt in soil water and of water in soil plotted against distance from high-tide mark (at Belle Plaine).

It seems likely that the growth of shrubs on the leeward side of the dunes is possible because the outer slopes deflect the wind upwards and the full effects of the salt-laden air are not felt by the plants growing on the tops of the taller dunes. That the winds sweep up over rather than across the summit of the taller dunes was shown by smoke experiments. The effect of wind is further shown by the fact that the typical *Coccoloba* association is not developed in the wind-swept valleys between the dunes, while the more exposed *Coccoloba* is planed off to a surface of leafless twigs, the whole surface having a slant towards the sea.

Some of the valleys between the dunes support *Coccoloba* on their landward slopes, but others continue right through the dunes with no more than the development of a poor scrub in their sheltered areas. Since there has been in the past some exploitation of the Belle Plaine *Coccoloba* wood for firewood, it seems quite probable that the removal of the shrub vegetation has resulted in the establishment of secondary successions in these areas.



# Observations on the sand dunes of Barbados

Further, these areas in which *Coccoloba* is entirely absent are invariably valleys, and the inference is that such valleys are 'blow-outs', caused by the removal of the vegetation cover.

The very extensive and deep root system of *Coccoloba uvifera* is worthy of note. The lateral roots extend for long distances, and at Belle Plaine the roots have been observed to reach downwards into the alluvial mud at the bottom of the dunes.

Frequency estimations for five sample areas are given below.

Shrubs	Growth form	Area					Frequency figure per 100
		I	II	III	IV	V	
<i>Caesalpinia bonducella</i>	P	—	f. (l.ab.)	—	—	—	12
<i>Calotropis procera</i>	P	f.	ab.	ab.	ab.	ab.	78
<i>Chrysobalanus icaco</i>	P	o.	f. (l.ab.)	f.	—	f.	44
<i>Coccoloba uvifera</i>	P	ab.	v.ab.	ab.	v.ab.	v.ab.	92
* <i>Cordia dichotoma</i>	P	o.	—	—	—	—	8
<i>Croton flavens</i>	P	f.	—	—	—	o. (l.f.)	20
<i>Hippomane mancinella</i>	P	o. (l.ab.)	f.	f. (l.ab.)	—	—	32
<i>Jatropha gossypifolia</i>	P	r.	—	—	—	—	4

\* Introduced about 200 years ago to Barbados and now widely naturalized in the island.

Low-growth forms	Growth form	Area					Frequency figure per 100
		I	II	III	IV	V	
<i>Canavalia maritima</i>	Ch	o. (l.ab.)	—	o. (l.ab.)	—	—	16
<i>Corchorus aestuans</i>	Th	r.	—	—	—	—	4
<i>Crotalaria pumila</i>	Ch	r.	—	r.	—	—	8
<i>C. retusa</i>	Th	o.	—	o.	—	—	16
<i>C. verrucosa</i>	Th	o.	—	—	—	—	8
<i>Cyperus rotundus</i>	G	o.	—	—	—	—	8
<i>Egletes prostrata</i>	Ch	r.	—	—	—	—	4
<i>Eleusine indica</i>	H	r.	—	—	—	—	4
<i>Euphorbia buxifolia</i>	Ch	o.	o. (l.f.)	f.	f.	—	40
<i>Ipomoea pes-caprae</i>	Ch	f.	ab.	ab.	f.	o.	64
<i>Lippia reptans</i>	Ch	o.	—	—	—	r. (l.f.)	12
<i>Pectis humifusa</i>	Ch	o.	—	r.	r.	—	16
<i>Philoxerus vermicularis</i>	Ch	—	—	—	—	r.	4
<i>Phyllanthus niruri</i>	Ch	r.	—	—	—	—	4
<i>Portulaca oleracea</i>	Ch	f.	—	—	—	—	12
<i>Sporobolus virginicus</i>	H	f. (l.ab.)	f.	f.	o.	o.	64
<i>Stachytarpheta indica</i>	Ch	—	—	r.	—	—	4
<i>Stenotaphrum secundatum</i>	Ch	o.	o.	o.	r.	f.	40
<i>Wedelia trilobata</i>	Ch	f. (l.v.ab.)	—	—	—	—	12

The table below shows frequency estimations for one sample area in the *Croton flavens* community.

Low-growth forms	Growth form	Frequency
<i>Corchorus aestuans</i>	Ch	o.
<i>Crotalaria pumila</i>	Ch	o.
<i>C. recusa</i>	Th	o.
<i>C. verrucosa</i>	Th	o.
<i>Cyperus rotundus</i>	G	o.
<i>Eleusine indica</i>	H	r.
<i>Euphorbia buxifolia</i>	Ch	o.
<i>Ipomoea pes-caprae</i>	Ch	f.
<i>Pectis humifusa</i>	Ch	o.
<i>Phyllanthus niruri</i>	Ch	o.
<i>Portulaca oleracea</i>	Ch	f.
<i>Sporobolus virginicus</i>	H	ab.
<i>Stenotaphrum secundatum</i>	Ch	f.
<i>Stylosanthes hamata</i>	Ch	f.
Shrubs		
<i>Calotropis procera</i>	P	f.
<i>Chrysobalanus icaco</i>	P	r.
<i>Coccoloba uvifera</i>	P	o.
<i>Croton flavens</i>	P	f.
<i>Hippomane mancinella</i>	P	r.

II. *Chancery Lane*

A beach, about  $1\frac{1}{2}$  km. in length, is backed by a strip of dune land some 50 m. in width and with a maximum height of about 6 m. In many places the foot of the dunes reaches high-tide mark. The beach faces south-east, but is fully exposed to the east-north-east trade winds blowing off the sea.

The sand is coarse grained and consists almost entirely of calcium carbonate (over 99%).

On part of the dunes coconut palms have been planted; this region was not investigated.

Behind the dunes at the southern end of the beach is a region of sour grass (*Andropogon pertusus* (L.) Willd.) pasture: to the northern end is a swamp, maintained artificially, and fringed by *Hippomane mancinella* L. and *Conocarpus erectus* L.

1. *Pioneer zone*. This zone extends, in some places, right down to the high-tide mark, and has a width of 5–10 m. in the southern area and as much as 25 m. in the northern area.

(a) *Soil*. The soil of this zone is, in those regions where it reaches the high-tide mark, liable to soaking by the sea. The coarse grain of the soil allows rapid evaporation of the water and the salt content may reach extremely high levels.

Soil samples collected at approximately mid-day showed the following figures:

Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
2 m.	1.470*	20.76	
10 m.	0.820	5.38	
20 m.	$\left\{ \begin{array}{l} 0.393 \\ 0.210 \\ 0.302 \end{array} \right.$	$\left\{ \begin{array}{l} 6.10 \\ 6.23 \\ 7.02 \end{array} \right.$	8.5
25 m.	$\left\{ \begin{array}{l} 0.121* \\ 0.201 \\ 0.105 \end{array} \right.$	$\left\{ \begin{array}{l} 10.81 \\ 4.26 \\ 6.32 \end{array} \right.$	8.5

\* Sample taken at high tide.

(b) *Floristic composition*. Only four plants occur in this zone. *Sporobolus virginicus* grows nearest to the sea margin, but is quickly followed by *Euphorbia buxifolia*. There is a little *Ipomoea pes-caprae* and very occasional *Pectis humifusa*. In the zone as a whole *Euphorbia buxifolia* is the most abundant plant, with *Sporobolus virginicus* also very frequent. These two plants form a fairly well covered association.

2. '*Ipomoea pes-caprae*' association. This zone varies in width from 10–15 m. The sand is well bound under a fairly close cover of vegetation.

(a) *Soil*. The figures for soil samples are:

Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
40 m.	$\left\{ \begin{array}{l} 0.24 \\ 0.28 \\ 0.30 \\ 0.22 \end{array} \right.$	$\left\{ \begin{array}{l} 13.30 \\ 6.20 \\ 5.93 \\ 5.20 \end{array} \right.$	8.0
50 m.	$\left\{ \begin{array}{l} 0.31 \\ 0.45 \\ 0.43 \\ 0.50 \end{array} \right.$	$\left\{ \begin{array}{l} 5.41 \\ 3.22 \\ 2.89 \\ 4.30 \end{array} \right.$	8.0

(b) *Floristic composition*. Species are few. There is rather less *Sporobolus virginicus* than at Belle Plaine, but considerably more *Euphorbia buxifolia*. The most conspicuous difference, however, is the occurrence in local patches of the shrubby *Tournefortia*

*gnaphalodes*, chiefly on the seaward side of the *Ipomoea pes-caprae* association. *Canavalia maritima* is entirely absent.

Low-growth forms	Growth form	Area			Frequency figure per 100
		I	II	III	
<i>Cyperus ligularis</i>	G	—	r.	—	7
<i>Euphorbia buxifolia</i>	Ch	ab.	v.ab.	ab.	87
<i>Ipomoea pes-caprae</i>	Ch	f.	v.ab.	v.ab.	87
<i>Pectis humifusa</i>	Ch	r. (l.ab.)	v.ab.	—	40
<i>Sporobolus virginicus</i>	H	f.	ab.	f.	67
<i>Stachytarpheta indica</i>	Ch	o.	—	r.	20
Shrubs					
<i>Tournefortia gnaphalodes</i>	P	v.ab.	o. (l.ab.)	—	40

3. '*Coccoloba*' association. The landward side of the dunes is more or less covered with an association dominated by *Coccoloba uvifera*.

(a) *Soil*. As at Belle Plaine this region had the dampest and the least saline soil, while the humus content was higher than in either of the preceding zones. Soil samples showed the following figures:

Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
80 m.	0.360	1.825	8.0
	0.751	1.720	
	1.451	0.830	
100 m.	0.860	0.587	
	1.738	0.325	

(b) *Floristic composition*. This association, like that at Belle Plaine, is very open on the seaward side and becomes closer towards the land. Here again the profile of stunted bushes, slanting towards the sea, and the more vigorous growth of shrubs on the sheltered side of the dunes, shows how the forward development of the association is hampered by the wind.

The main differences between this association and that of Belle Plaine are that *Calotropis procera* is absent from Chancery Lane, while the undergrowth here is better developed (though still scanty), consisting chiefly of *Stachytarpheta indica* and *Cyperus ligularis*.

Low-growth forms	Growth form	Area			Frequency figure per 100
		I	II	III	
<i>Cyperus ligularis</i>	G	—	o.	o.	26
<i>Euphorbia buxifolia</i>	Ch	r.	—	f.	26
<i>Ipomoea pes-caprae</i>	Ch	r.	f.	v.ab.	60
<i>Pectis humifusa</i>	Ch	o.	r.	—	20
<i>Sporobolus virginicus</i>	H	—	v.r.	—	3
<i>Stachytarpheta indica</i>	Ch	o.	ab.	o.	53
Shrubs					
<i>Capraria biflora</i>	P	—	f.	o.	33
<i>Caesalpinia bonducella</i>	P	r. (l.ab.)	r.	o.	26
<i>Coccoloba uvifera</i>	P	v.ab.	v.ab.	f.	87
<i>Hippomane mancinella</i>	P	v.ab.	—	o.	47
<i>Lantana involucrata</i>	P	—	r.	—	7
<i>Tecoma leucoxydon</i>	P	—	r.	—	7
<i>Tournefortia gnaphalodes</i>	P	o.	—	—	13

### III. Silver Sands

This is a stretch of beach about 400 m. in length, facing south-south-east, and carrying, particularly in the more easterly section, a considerable development of dunes. The adjacent land is flat and the trade wind sweeps across the whole area with some force.

The dune vegetation here is backed in places by a flat open association with *Melanthera deltoidea* and *Lippia reptans*. This is of interest, as Stehlé describes an association of *Melanthera deltoidea* and *Lippia nodiflora* as typically developed behind the *Coccoloba* association of Guadeloupe (Stehlé, 1939).

1. *Pioneer zone.*

(a) *Soil.* As at Chancery Lane the soil contains over 99% of calcium carbonate. Analysis figures are as follows:

Conditions	Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
Damp day: high tide	2 m.	4.399	9.35	8.5
	5 m.	3.202	8.24	
Damp day: low tide	20 m.	0.532	6.38	8.5
		0.918	5.06	
Dry day: high tide	2 m.	3.823	8.78	8.5
	5 m.	2.032	10.11	
Dry day: low tide	20 m.	0.108	9.74	8.5
		0.254	8.46	

(b) *Floristic composition.* The pioneers here are *Sporobolus virginicus* and *Euphorbia buxifolia*. These, singly or together, form small clumps near the high-tide mark, while on the landward side the association becomes closer, being invaded by *Ipomoea pes-caprae* and giving rise to the *Ipomoea* association. The pioneer zone varies in width from 5–20 m.

2. *Ipomoea pes-caprae* association. This has a width of 20–30 m.

(a) *Soil.* Samples gave the following figures:

Conditions	Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
Damp day: high tide	40 m.	4.321	0.471	8.0
	45 m.	4.802	0.420	
Damp day: low tide	40 m.	1.820	0.98	8.0
	50 m.	3.632	0.63	
Dry day: high tide	40 m.	0.426	3.25	8.0
	45 m.	0.298	2.90	
Dry day: low tide	40 m.	0.351	3.72	8.0
		0.396	2.81	
	50 m.	0.520	1.98	
		0.401	2.65	

(b) *Floristic composition.* *Euphorbia buxifolia* is the next most abundant plant to *Ipomoea pes-caprae*, and there is less *Sporobolus virginicus* than at either Belle Plaine or Chancery Lane. Over about half the length of this association, on the seaward edge, is an abundant growth of *Tournefortia gnaphalodes*.

Low-growth forms	Growth form	Area		Frequency figure per 100
		I	II	
<i>Cyperus ligularis</i>	G	f.	o.	70
<i>Euphorbia buxifolia</i>	Ch	f.	v.ab.	80
<i>Ipomoea pes-caprae</i>	Ch	v.ab.	v.ab.	100
<i>Pectis humifusa</i>	Ch	o.	ab.	60
<i>Sporobolus virginicus</i>	H	o.	f.	50
<b>Shrubs</b>				
<i>Lantana involucrata</i>	P	—	f.	30
<i>Melanthera deltoidea</i>	P	—	r.	10
<i>Tournefortia gnaphalodes</i>	P	v.ab.	—	50

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3. '*Coccoloba*' association. The *Coccoloba* association occupies the top of the tallest dunes and the sheltered regions behind them, and the same effects of wind are conspicuous here as at Belle Plaine and at Chancery Lane.

(a) *Soil*. Samples gave the following figures:

Conditions	Distance from sea	Percentage of water in soil	Percentage of salt in soil water	pH
Damp day: high tide	80 m.	5.125	0.683	—
Damp day: low tide	80 m.	5.382	0.421	—
Dry day: low tide	80 m.	1.283	0.350	8.0
		2.370	0.112	

(b) *Floristic composition*. The *Coccoloba* association at Silver Sands changes as the beach is followed from south-west to north-east. The south-west end consists chiefly of *Hippomane mancinella*, *Tecoma leucoxydon* and *Caesalpinia bonducella*, with undergrowth, while the north-east end consists chiefly of *Coccoloba*, and has few other shrubs. The *Coccoloba* association here is much less open than at Belle Plaine and Chancery Lane.

Low-growth forms	Growth form	Area		Frequency figure per 100
		I	II	
<i>Cyperus ligularis</i>	G	o.	—	20
<i>Ipomoea pes-caprae</i>	Ch	o.	—	20
<i>Lippia reptans</i>	Ch	v.r.	—	5
<i>Pectis humifusa</i>	Ch	r.	—	10
<i>Sporobolus virginicus</i>	H	r.	—	10
<i>Stachytarpheta indica</i>	Ch	o.	—	20
Shrubs				
<i>Caesalpinia bonducella</i>	P	—	o.	20
<i>Calotropis procera</i>	P	v.r.	—	5
<i>Capraria biflora</i>	P	v.r.	—	5
<i>Coccoloba uvifera</i>	P	v.ab.	r.	60
<i>Cordia dichotoma</i>	P	v.r.	—	5
<i>Hippomane mancinella</i>	P	—	f.	30
<i>Lantana involucrata</i>	P	o.	—	20
<i>Melanthera deltoidea</i>	P	v.r.	—	5
<i>Tecoma leucoxydon</i>	P	—	v.ab.	50

Area I was near the south-west end of the beach, while Area II was near the north-east end.

### IV. *Enterprise* (Cotton House Bay)

In a small bay, about 200 m. long, defined by low coral cliffs, a narrow beach, now about 25 m. wide at its broadest, has made its appearance during the past 12 years. The area is sheltered from the trade winds and there has been no dune formation, but it has been possible to see some of the early stages of seashore colonization.

The beach first emerged as a true beach, not entirely covered at high tide, about 1933, and year by year has gradually widened. From its very first appearance there has been sporadic colonization by seedlings, mostly of *Hippomane mancinella*, from the trees which fringe the low cliffs bordering the beach. These seedlings are short-lived and have never yet shown signs of becoming established.

In 1937 the first tufts of semi-permanent vegetation appeared—small patches of *Sporobolus virginicus*. These gained a firmer footing by 1938, and in that year another grass, *Chloris* sp., appeared as scattered and not very thriving individuals. By 1939 there were a few plants of *Ipomoea pes-caprae*, and the *Sporobolus virginicus* was pushing out

towards the gradually receding high-tide mark. On the last occasion that this area was studied there was, in places, a well-marked zone of *Sporobolus virginicus* followed by a poorly developed region of *Ipomoea pes-caprae* amongst which were a few individuals of *Cyperus ligularis* and *Chloris* sp.

#### V. Maxwell's Coast

From about the end of the last century until 1932 there was a rapidly growing beach in this region, and the vegetation followed the sea—the zonation being very similar to that of the sand dunes of Chancery Lane or Silver Sands. There was a pioneer zone of *Sporobolus virginicus* and *Euphorbia buxifolia* followed by a wide zone of *Ipomoea pes-caprae* and other herbaceous plants, which was generally flanked on the seaward side by *Tournefortia gnaphalodes*. In some places a *Coccoloba* association was appearing.

From 1932 rapid sea encroachment has been taking place, and a reverse succession has been brought about. During the roughest weather (the main erosion is by southerly gales in the wet season) the whole pioneer zone is destroyed and the beach cut back as far as or further than the *Tournefortia gnaphalodes* of the *Ipomoea* zone. In those years when erosion is least readjustment of the vegetation takes place: the *Ipomoea*, *Tournefortia* and other members of the *Ipomoea* zone in the regions nearest the sea die, except *Sporobolus virginicus* and *Euphorbia buxifolia*, which survive to form a zone similar to the pioneer zone of other beaches, while seedlings of *Tournefortia gnaphalodes* appear towards the seaward margin of the surviving *Ipomoea*. Year by year these zones can be seen, sometimes very much telescoped into each other, at other times clearly defined, keeping pace with the return of the sea.

#### DISCUSSION AND CONCLUSIONS

A close parallel has been shown to exist between the vegetation of the three dune areas described. A division into pioneer, *Ipomoea* and *Coccoloba* zones has been possible in each case: the use of the word 'pioneer' for the zone nearest the sea implies that the zones are successive stages of a sere.

Hardy (1934) has described the stages of sand-dune formation in Barbados, and names *Sporobolus virginicus* and *Euphorbia buxifolia* as the plants most important in stabilizing the sand. The general sequence of events then resembles that described for Britain (Tansley, 1911).

The observations made by the writer at Cotton House Beach, described above, show the common pioneer zone plant of the dunes, *Sporobolus virginicus*, actually leading the colonization of virgin beach, and being followed by the dominant plant of the second dune zone, *Ipomoea pes-caprae*. This leaves little room for doubt that the zonation of the dunes is truly the zonation of a sere.

The fact that these zones are stages in a sere does not, however, necessarily imply that forward progression is always taking place. Maxwell's Beach has clearly shown that exactly the same sequence of zones can occur when the whole succession is retreating.

There is no evidence that at any of the three dune areas under consideration there has been any major change in historical times: neither advance to the sea nor encroachment

by the sea are recorded. Undoubtedly small local changes take place. New patches of foreshore become colonized and the succession creeps forward over a small area; other areas lose their vegetation as a result of blow-outs, or extra high tides, etc. (annual serial transects at Belle Plaine have shown the relatively unstable nature of the pioneer zone and forward regions of the *Ipomoea pes-caprae* zone), but the general character of the vegetation of each community remains unchanged: the community as a whole is stable.

The soil figures show that there is a general increase in water content as distance from the sea increases, except in the case of those samples taken very close to the sea margin at high tide. This is probably related to the increasing humus content of the soil. The water content of the soil is generally extremely low, but increases rapidly at increasing depth, and the low water content at a depth of 15 cm. will be important only to seedlings which may have to survive such conditions for many successive days.

Further, although the physical characteristics of the soil may make what little moisture there is readily available to plants, the high salinities, particularly in the pioneer and *Ipomoea* zones, must limit the flora to plants which show very great tolerance to salt. The most striking differences for the three vegetation zones are shown by the salt figures: low water-content of the soil, combined with exposure to continuous sea spray and surface evaporation of the loosely held water of a sandy surface, produce an extremely saline soil water, particularly in the regions nearest the sea: a reaction to this is seen in the high suction pressures developed in the plants growing in these regions. Measurements carried out on leaves of *Ipomoea pes-caprae*, *Tournefortia gnaphalodes* and *Philoxerus vermicularis* gave suction pressures of 80–100 atmospheres in each case. (The suction pressures were measured by tissue shrinkage methods, both microscopic and macroscopic.)

The highest concentration of salt recorded in the *Coccoloba* zone was 1.825% of the soil water, while the average for this zone was 0.595%. This is in striking contrast to the average for the *Ipomoea* zone which is 3.14%, and this is markedly less than the average for the pioneer zone, which, even excluding the abnormally high figure given at high tide at Chancery Lane, is 6.62%. With these great differences it is perhaps justifiable to conclude that salt concentration is the most important single factor limiting the forward spread of the vegetation.

The salt concentration in the soil water is itself the result of a number of factors. It is doubtful whether much is drawn upwards from underlying salt water, particularly in the *Ipomoea* and *Coccoloba* zones. Hardy, at Maxwell's Coast, which is a low strip of sand without dune formation, found the water table to be 75 cm. below soil level and the salt concentration in the water at this depth only 0.05%. These tests were made at a distance of 50 m. from high-tide mark—a distance corresponding to the pioneer zone at Belle Plaine and the *Ipomoea* zone at the other dune localities. The main source of salt in the surface layers of the sand is undoubtedly the sea spray: spray which is evaporated almost as soon as it is blown on to the warm sand, which is in fact often visibly salt encrusted. The falling off in salt concentration in the soil water towards the landward side of the beach is due to two factors:

- (i) less salt spray is deposited as distance from the sea increases;
- (ii) the water-retaining capacity of the soil increases with increasing distance from the sea, and therefore the salt solution will be more dilute.

Mean figures obtained at Belle Plaine illustrate these facts:\*

Distance from sea	Percentage of salt in sand	Percentage of water in soil	Percentage of salt in soil water
50 m.	0.0128	0.241	5.30
100 m.	0.0082	0.482	1.79
150 m.	0.0064	1.650	0.39

The increase in water-retaining capacity of the soil is, as previously mentioned, probably due to the accumulation of humus. No quantitative data were obtained for the humus content of the soils, but the following facts were noted:

- (i) microscopic examination of soils for all three areas showed a definite and considerable increase in humus content as distance from the sea increased;
- (ii) the accumulation of humus is extremely slow. The sand-dune plants are nearly all evergreens (annuals are few and the only deciduous plant on the dunes is *Tecoma leucoxydon*) and there is little deposition of litter, while in the dry soil decomposition of dead plant material is far from rapid;
- (iii) considerable amounts of freshly blown sand were found to accumulate on the surface of the soil within the *Coccoloba* association, while less was observed in the *Ipomoea* association. (It would seem that for relative stability of the vegetation type an equilibrium between the rate of humus deposition and accumulation of sand must be reached.)

The effect of the salt-laden wind has already been mentioned. Apart from blowing spray on to the sand and thus maintaining the salinity of the soil, its drying and possibly toxic effect on the buds and leaves of the shrubs, particularly *Coccoloba*, clearly limits the forward spread of these plants. This limiting effect, however, is only definite when operating in conjunction with the scant water supply of the dunes. Under different soil conditions, e.g. the fine grained and moist clays of the Newcastle coastline, *Coccoloba* grows close to the sea.

The small decrease in pH as distance from the sea grows greater is, no doubt, the result of humus accumulation and is probably of little or no importance in determining the composition of the flora.

The plants of the Barbados sand dunes all show many of the features associated with halophytes, psammophytes and zerophytes in general: the superficial features of some are described by Hardy (1934). They are, in general, clearly well adapted to survive in their conditions of actual and physiological drought, and some can survive, for short periods at any rate, conditions of very great salinity.

In the three areas examined two had very highly calcareous soil, while the third (Belle Plaine) was predominantly siliceous—a fact which is perhaps reflected in the lower pH for the *Coccoloba* zone in this area. A comparison of their floristic composition shows the considerable similarity in the vegetation of each locality, and the only differences that might possibly be related to the chemical differences of the soil are:

- (i) the extensive appearance of *Philoxerus vermicularis* as the chief pioneer at Belle Plaine, and its non-appearance in the other localities;
- (ii) the greater number of species at Belle Plaine, thirty-one as compared with twelve for Chancery Lane and seventeen for Silver Sands.

With regard to (i), the appearance of *Philoxerus vermicularis* as a pioneer plant is interesting. It does not seem to be typical of this habitat elsewhere, and is quoted by

\* See Fig. 2.



Stehlé as following a *Melanthera deltoidea*-*Lippia nodiflora* association on clayey soils in Guadeloupe. In Barbados, however, on the whole stretch of siliceous sand from Bath to Morgan Lewis *Philoxerus vermicularis* is the commonest pioneer.

With regard to (ii), the following plants are found at Belle Plaine, but not on the other two beaches:

<i>Canavalia maritima</i> (Aubl.) Thou.	<i>Eleusine indica</i> (L.) Gaertn.
<i>Corchorus aestuans</i> L.	<i>Jatropha gossypifolia</i> L.
<i>Chrysobalanus icaco</i> L.	<i>Philoxerus vermicularis</i> Beauv.
<i>Crotalaria pumila</i> Orteg.	<i>Phyllanthus niruri</i> L.
<i>C. retusa</i> L.	<i>Portulaca oleracea</i> L.
<i>C. verrucosa</i> L.	<i>Sesuvium portulacastrum</i> L.
<i>Croton flavens</i> L.	<i>Stenotaphrum secundatum</i> (Walt.) Ktze.
<i>Cyperus rotundus</i> L.	<i>Stylosanthes hamata</i> Taut.
<i>Egletes prostrata</i> (Sw.) Ktze.	<i>Wedelia trilobata</i> (L.) Hitchc.

Every one of the above plants has a wide distribution on coral limestone soils in other localities in the island, with the exceptions of *Chrysobalanus icaco*, *Egletes prostrata* and *Stenotaphrum secundatum*. The last named appears to be confined to the sandy soils at and near Belle Plaine; *Chrysobalanus icaco* is confined to the siliceous soils of the 'Scotland district', and Stehlé (1939) mentions *Egletes prostrata* as characteristic of the non-calcareous sands of Guadeloupe.

The differences in chemical composition of the soils of Belle Plaine, Chancery Lane and Silver Sands thus seem to affect the vegetation little: the non-siliceous nature of the sand at the two latter places may exclude possibly three species.

#### SUMMARY

1. Three sand dune areas in Barbados are described in some detail and two other seashore localities are briefly mentioned.

2. Three more or less clear vegetation zones running parallel with the sea margin are traced: a pioneer zone with *Sporobolus virginicus*, *Euphorbia buxifolia* and *Philoxerus vermicularis* as its important members, followed by a zone dominated by *Ipomoea pes-caprae*, and finally a zone dominated by *Coccoloba uvifera*. There is a progression from low to higher growth forms as distance from the sea increases.

3. Soil analyses show that:

- (i) the water contents and concentrations of salt in water at 15 cm. depth are more or less similar in the corresponding vegetation zones of the three areas;
- (ii) as distance from the sea increases
  - (a) the moisture content of the soil increases,
  - (b) the salt concentration in the soil water decreases,
  - (c) the pH decreases.

4. The vegetation zones may be regarded as stages in a sere, but are held in a comparatively stable condition by topographic factors.

#### Comparison of frequency figures for Belle Plaine, Chancery Lane and Silver Sands

	Family	Belle Plaine	Chancery Lane	Silver Sands
<i>Pioneer Zone</i>				
Low-growth forms:				
<i>Euphorbia buxifolia</i> Lam.	Euphorbiaceae	—	40	10
<i>Ipomoea pes-caprae</i> (L.) Sweet	Convolvulaceae	—	2	2
<i>Pectis humifusa</i> Sw.	Compositae	—	1	—
<i>Philoxerus vermicularis</i> Beauv.	Amaranthaceae	5	—	—
<i>Sesuvium portulacastrum</i> L.	Aizoaceae	1	—	—
<i>Sporobolus virginicus</i> (L.) Ktz.	Gramineae	5	30	10

Family		Belle Plaine	Chancery Lane	Silver Sands
<i>'Ipomoea pes-caprae' Association</i>				
(a) Low-growth forms:				
Canavalia maritima (Aubl.) Thou.	Leguminosae	10	—	—
Corchorus aestuans L.	Tiliaceae	5	—	—
Cyperus ligularis L.	Cyperaceae	—	7	70
Euphorbia buxifolia Lam.	Euphorbiaceae	60	87	20
Ipomoea pes-caprae (L.) Sweet	Convolvulaceae	95	87	100
Lippia reptans Kth.	Verbenaceae	10	—	—
Pectis humifusa Sw.	Compositae	25	40	60
Philoxerus vermicularis Beauv.	Amaranthaceae	5	—	—
Portulaca oleracea L.	Portulacaceae	15	—	—
Sporobolus virginicus (L.) Ktz.	Gramineae	95	67	50
Stachytarpheta indica Vahl.	Verbenaceae	—	—	20
Stenotaphrum secundatum (Walt.) Ktz.	Gramineae	35	—	—
(b) Shrubs				
Calotropis procera R. Br.	Asclepiadaceae	15	—	—
Chrysobalanus icaco L.	Rosaceae	10	—	—
Coccoloba uvifera L.	Polygonaceae	10	—	—
Lantana involucrata L.	Verbenaceae	—	10	30
Melanthera deltoidea Michx.	Compositae	—	—	20
Tournefortia gnaphalodes R. Br.	Boraginaceae	15	40	50
<i>'Coccoloba' Association</i>				
(a) Low-growth forms:				
Canavalia maritima (Aubl.) Thou.	Leguminosae	16	—	—
Corchorus aestuans L.	Tiliaceae	4	—	—
Crotalaria pumila Orteg	Leguminosae	8	—	—
C. retusa L.	Leguminosae	16	—	—
C. verrucosa L.	Leguminosae	8	—	—
Cyperus ligularis L.	Cyperaceae	—	26	20
C. rotundus L.	Cyperaceae	8	—	—
Egletes prostrata (Sw.) Ktz.	Compositae	4	—	—
Eleusine indica (L.) Gaertn.	Gramineae	4	—	—
Euphorbia buxifolia Lam.	Euphorbiaceae	40	26	—
Ipomoea pes-caprae (L.) Sweet	Convolvulaceae	64	60	20
Lippia reptans Kth.	Verbenaceae	12	—	5
Pectis humifusa Sw.	Compositae	16	20	10
Philoxerus vermicularis Beauv.	Amaranthaceae	4	—	—
Phyllanthus niruri L.	Euphorbiaceae	4	—	—
Portulaca oleracea L.	Portulacaceae	12	—	—
Sporobolus virginicus (L.) Ktz.	Gramineae	64	53	20
Stachytarpheta indica Vahl.	Verbenaceae	4	53	20
Stenotaphrum secundatum (Walt.) Ktz.	Gramineae	40	—	—
Stylosanthes hamata Taut.	Leguminosae	8	—	—
Wedelia trilobata (L.) Hitchc.	Compositae	12	—	—
(b) Shrubs:				
Caesalpinia bonducella Flem.	Leguminosae	12	26	20
Calotropis procera R. Br.	Asclepiadaceae	76	—	5
Capraria biflora L.	Scrophulariaceae	—	33	5
Chrysobalanus icaco L.	Rosaceae	44	—	—
Coccoloba uvifera L.	Polygonaceae	92	87	60
Cordia dichotoma Forst.	Boraginaceae	8	—	5
Croton flavens L.	Euphorbiaceae	20	—	—
Hippomane mancinella L.	Euphorbiaceae	32	47	30
Jatropha gossypifolia L.	Euphorbiaceae	4	—	—
Lantana involucrata L.	Verbenaceae	—	7	20
Melanthera deltoidea Michx.	Compositae	—	—	5
Tecoma leucoxydon Mart.	Bignoniaceae	—	7	50
Tournefortia gnaphalodes R. Br.	Boraginaceae	—	13	—

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## STUDIES ON THE VEGETATION OF MAURITIUS

## IV. SOME NOTES ON THE INTERNAL CLIMATE OF THE UPLAND CLIMAX FOREST

BY R. E. VAUGHAN AND P. O. WIEHE

*(With three Figures in the Text)*

## INTRODUCTION

The object of the investigation described in this paper was to secure some meteorological data for the interior of the upland climax forest of Mauritius and to study and compare the results obtained with the normal or standard climate outside the forest. The preparation of this paper has been much delayed and its scope reduced as both authors have been engaged on work in connexion with the war. It was intended to determine the vertical gradients of certain meteorological elements with a view, *inter alia*, to the study of epiphyte distribution but, owing to the lack of the necessary apparatus and material, this part of the investigation has been deferred.

The meteorological elements chosen for special study were temperature, humidity and rainfall and it was decided that the most suitable site was in the Upland climax forest of Macabé which was the subject of the previous paper in this series (Vaughan & Wiehe, 1941). A Stevenson screen of the standard type described in *The Observer's Handbook* (1926) was set up and fitted with maximum and minimum and wet and dry bulb thermometers, while underneath the thermometer house a second compartment of similar dimensions was built to accommodate a Casella thermo-hygrograph. Three 4-in. rain gauges were installed at random on the forest floor at intervals of about 10 yards from the screen.

The exposed station was sited in a clearing outside the forest at a distance of about half a mile from the forest station and comprised a rain gauge and a second Stevenson screen with the four thermometers. The instruments were checked against standards at the Royal Alfred Observatory, and we take this opportunity to express our thanks to the Director and his staff for the loan and testing of thermometers and the provision of data for other localities.

The observations in the forest were taken over a period of 15 months from January 1939 to March 1940, the screens having been set up in the previous November to allow preliminary readings to be obtained and a general check on the instruments made. Readings were taken every day at 10.00 hr. Mauritius civil time. The thermo-hygrograph was installed in April 1940, and at the end of 12 months in the forest was transferred to the exposed station for 6 months.

To obtain further data for the normal climate outside the forest, readings from two other stations have been utilized. One of these is at Curepipe Botanic Gardens where records have been kept for a continuous period of 48 years, and the other at the Royal College, Curepipe, where observations were begun in 1931 and include recordings from a thermo-hygrograph similar in pattern to the one used at the forest station. Both these stations are situated on the upland plateau about 8 miles from the forest.

## THE CLIMATE OF THE UPLANDS

The general climate of the Uplands has been described in two previous papers by the present authors (Vaughan & Wiehe, 1937, 1939) and although no data are available for the area in the immediate vicinity of the Macabé forest, the recordings provided by Curepipe Gardens give a fairly accurate picture of the climate in the Uplands as a whole, though the rainfall is probably rather higher than that which prevails over the forest. In brief, the upland climate in the region of the climax forest is characterized by a high, very variable, annual rainfall of about 125 in. (306 cm.), a moderate temperature with a mean annual value of 68° F. (20° C.), and a high relative humidity of 85-90% of saturation.

A commonly adopted method for illustrating rainfall and temperature, enabling an immediate comparison to be made with other climates, is the hydrotherm of Raunkier (1935) in which the rainfall in centimetres and the temperature in degrees centigrade are represented on the same ordinate and plotted against the month of the year. A hydrotherm has been constructed based on the adopted normals for Curepipe Gardens and is shown in Fig. 1.

## PRESENTATION OF DATA AND DISCUSSION

The results obtained at the two sites may be conveniently considered under three heads: temperature, rainfall and humidity.

*Temperature*

The figures set out in Table 1 show the mean daily maximum temperature for the month at the exposed station (A), and the forest station (B), cols. 1 and 2; the difference between them, col. 3; the corresponding minima and difference, cols. 4, 5 and 6; the mean temperature and difference, cols. 7, 8 and 9; and finally, the mean range of temperature for the month at the two stations, cols. 10 and 11.

The mean annual temperature over the forest area is probably not far removed from 68° F. (20° C.) which is the value for Curepipe Gardens. For the year 1939 the mean temperature at the exposed station was 68° F. (20° C.) whereas at Curepipe Gardens for the same period it was 70.2° F. (21.2° C.). The altitude 550 m. (1800 ft.) and latitude 20° S. of the forest render the temperature more seasonal than that of typical tropical climates, for example British Guiana and New Hebrides, where intensive ecological studies of evergreen tropical forest have been made. It is probable that the more seasonal temperature of the upland climax forest in Mauritius and its comparatively low winter value have been important factors in determining those distinctive characters which distinguish it from typical tropical rain-forest.

Before examining the data given in Table 1, the results obtained in other tropical forests may be reviewed briefly. Several workers in tropical regions have secured comparative data between the forest and normal or standard climates. Shreve (1914), working in the Blue Mountain forests of Jamaica at about 1500 m. (5000 ft.) lat. 18° N., found there was an average daily range of 5.3° F. (3° C.) and 7.1° F. (4° C.) in two different localities of the forest, with a corresponding range of 12-13° F. in forest clearings; these results are comparable with those obtained by Allee (1926) in the forests of Panama. Carter (1934) in the rain-forest of British Guiana obtained a diurnal range of 5.5-9° F.

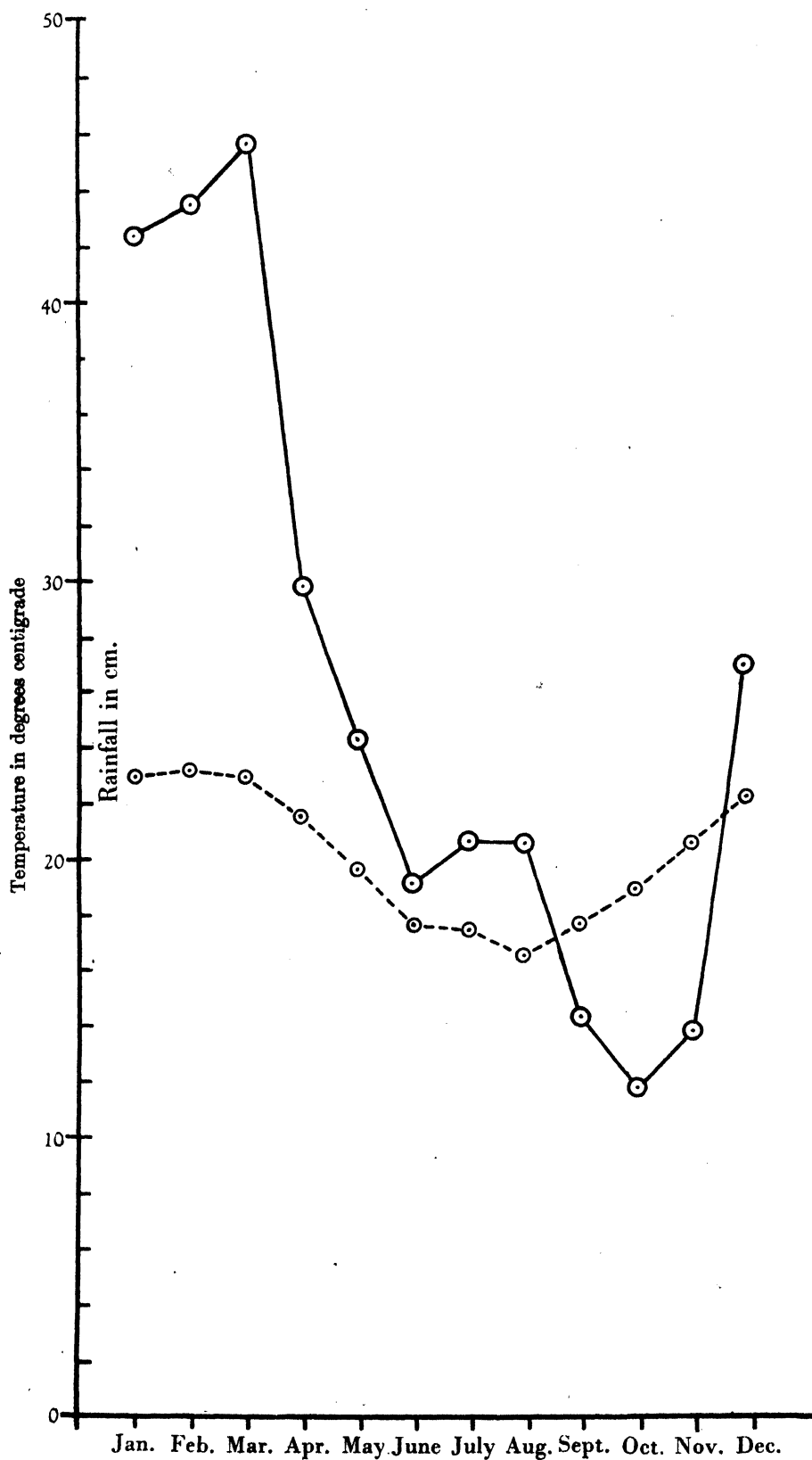


Fig. 1. Hydrotherm for Curepipe Gardens, Mauritius. Rainfall, continuous line; temperature, broken line.

(3–5° C.). Moreau (1935) in the closed evergreen forest at Amani, Tanganyika, found that the temperature was more equable in the forest with almost the same minima, but with the maxima about 5·4° F. (3° C.) lower all the year round and concludes: 'the potentially significant divergence from the standard climate is in the maxima and daily range and not in the minima'. This conclusion was borne out by Baker and Harrison (1936) who, in referring to the tropical rain-forest of Hog Harbour, New Hebrides, lat. 15° S. remark 'the minima in the forest were nearly similar to the minima in the screen at the sunshine station but the forest maxima were always much below the maxima in the screen'. It was shown that the difference between maxima and minima remained fairly constant throughout the year at roughly 5° F. (2·7° C.).

Table 1. *Temperature (° F.) at exposed station A and forest station B for the year 1939*

Readings taken at 10.00 hr., Mauritius Civil Time

	Mean of daily maxima for the month		Diff. A-B (3)	Mean of daily minima for the month		Diff. A-B (6)	Mean for the month*		Diff. A-B (9)	Range A	Range
	A (1)	B (2)		A (4)	B (5)		A (7)	B (8)		(10) Cols. 1-4	(11) Cols. 2-5
Jan.	82·3	73·5	8·8	64·9	64·5	0·4	73·2	68·5	4·7	17·4	9·0
Feb.	82·4	75·5	6·9	67·1	66·6	0·5	74·3	70·6	3·7	15·3	8·9
March	81·2	74·6	6·6	68·2	68·0	0·2	74·1	70·8	3·3	13·0	6·6
April	78·0	72·9	5·1	65·6	65·5	0·1	71·3	68·7	2·6	12·4	7·4
May	75·0	67·6	7·4	62·2	61·7	0·5	68·1	64·1	4·0	12·8	5·9
June	71·5	63·5	8·0	57·9	56·4	1·5	64·4	59·5	4·9	13·6	7·1
July	66·0	63·2	2·8	57·9	57·7	0·2	61·4	60·0	1·4	8·1	5·5
Aug.	67·1	61·7	5·4	56·1	57·7	-1·6	61·1	58·2	2·9	11·0	4·0
Sept.	70·2	64·7	5·5	57·8	57·9	-0·1	63·4	60·8	2·6	12·4	6·8
Oct.	73·7	66·5	7·2	58·9	57·6	1·3	65·6	61·6	4·0	14·8	8·9
Nov.	75·8	69·5	6·3	61·2	59·9	1·3	67·9	64·3	3·6	14·6	9·6
Dec.	78·1	74·0	4·1	65·7	65·4	0·3	71·4	68·8	2·6	12·4	8·6
Mean	75·1	68·9	6·2	61·9	61·5	0·4	68·0	64·6	3·4	13·2	7·4

\* Mean temperature obtained from 0·5 (max. + min.) - 0·5° F.; probably does not differ by more than 0·1° F. from mean temperature from hourly values.

Highest temperature recorded (A) 87·9° F. on 25 March; (B) 77·6° F. on 25 Feb.

Lowest temperature recorded (A) 51·6° F. on 1 Sept.; (B) 51·8° F. on 1 Sept.

The temperature recordings for the forest and exposed station in Mauritius may now be considered. The mean temperature for the year in the forest was found to be 64·6° F. (18·1° C.), 3·4° F. below the mean for the exposed station. The highest mean temperature for the month for the exposed station was 74·3° F. (23·5° C.) which was registered in February, the lowest mean temperature 61·1° F. (16·2° C.) occurred in August. At the forest station the highest mean was 70·8° F. (21·6° C.) in March and the lowest, in August, 58·2° F. (14·6° C.).

The most significant figures are those showing the difference between maxima and minima at the two stations (Table 1, cols. 3 and 6) and the monthly range of temperature (cols. 10 and 11). The mean of the monthly maxima in the forest was 6·2° F. (3·3° C.) below the value obtained for the exposed station, whereas the mean of the monthly minima for the forest was only 0·4° F. below the corresponding figure outside the forest. The mean maximum and minimum temperatures for each month are expressed graphically

in Fig. 3. When the figures for the absolute maxima and minima are compared, that is the mean of the highest and lowest temperatures recorded in each month, the difference between the maxima and minima becomes still more pronounced; in this case the absolute maximum differed by  $8.2^{\circ}$  F. ( $4.6^{\circ}$  C.) while the absolute minimum of the forest was only  $0.6^{\circ}$  F. below that of the exposed station.

Turning now to the range of temperatures experienced at the two stations it is found that the forest station has a mean monthly range of  $7.4^{\circ}$  F. ( $4.1^{\circ}$  C.), little more than half the value obtained for the exposed station. The range appears to be somewhat greater at both stations during the summer months. The absolute maximum range of temperature outside the forest during the year, that is the difference between the highest and lowest temperatures recorded, was  $36.3^{\circ}$  F. ( $20.2^{\circ}$  C.) whereas the maximum range that occurred on any one day was  $22.2^{\circ}$  F. ( $12.3^{\circ}$  C.); the corresponding figures for the forest station were  $25.8^{\circ}$  F. ( $14.3^{\circ}$  C.) and  $14.5^{\circ}$  F. ( $8.1^{\circ}$  C.) respectively.

To enable a rapid appreciation and comparison to be made of the magnitude of the daily range and the temperature gradient experienced in the forest throughout the year with the seasonal climate of temperate regions, the maximum and minimum temperatures for every day of the year have been plotted vertically (pin-headed lines) together with the values for London for the same period (Fig. 2).

A study of the thermograph curves provides an interpretation of the data obtained for the maximum and minimum temperatures as recorded in Table 1, and the results taken as a whole make it possible to give a tentative explanation of the difference between the external and internal climates. The thermograph trace reveals that the 24 hr. daily march of temperature is usually built up of three distinct phases. Beginning soon after sunrise there is a rapid increase of temperature to the maximum value which is reached about 13.00–13.30 hr., then a fairly steep fall takes place until 19.00 hr. followed by a much more gradual decrease during the hours of darkness to the minimum temperature shortly before sunrise. In the forest it was found that the sudden morning increase of temperature was usually an hour or more later than that at the exposed station, and that the maximum value was not reached until 14.30 or 15.00 hr. and quite often as late as 16.00 hr.; from then until 20.00–21.00 hr. the corresponding rapid fall took place.

During the hours of darkness more or less uniform conditions of temperature prevail both in the interior of the forest and in the atmosphere immediately above it, conditions that is of low temperature and maximum humidity. The sudden increase of temperature which takes place during the morning is delayed in the forest owing to the prevention of insolation by the dense cover and the stillness of the atmosphere; as a result, the outside air reaches its maximum while the forest temperature is still increasing. During the late afternoon the rapidly falling outside temperature will overtake that of the forest and, in consequence, vertical convection currents set in and intermingling of the warmer forest air and external atmosphere takes place. In this way a more or less uniform temperature is re-established by nightfall and a gradual decrease continues during the night until the minimum temperature is reached the following morning.

### *Rainfall*

The measurements for rainfall and relative humidity are given in Table 2; this shows the relative humidity for the two stations, cols. 1 and 2; the difference between them, col. 3; the rainfall at the exposed station and that registered by the three forest rain gauges,

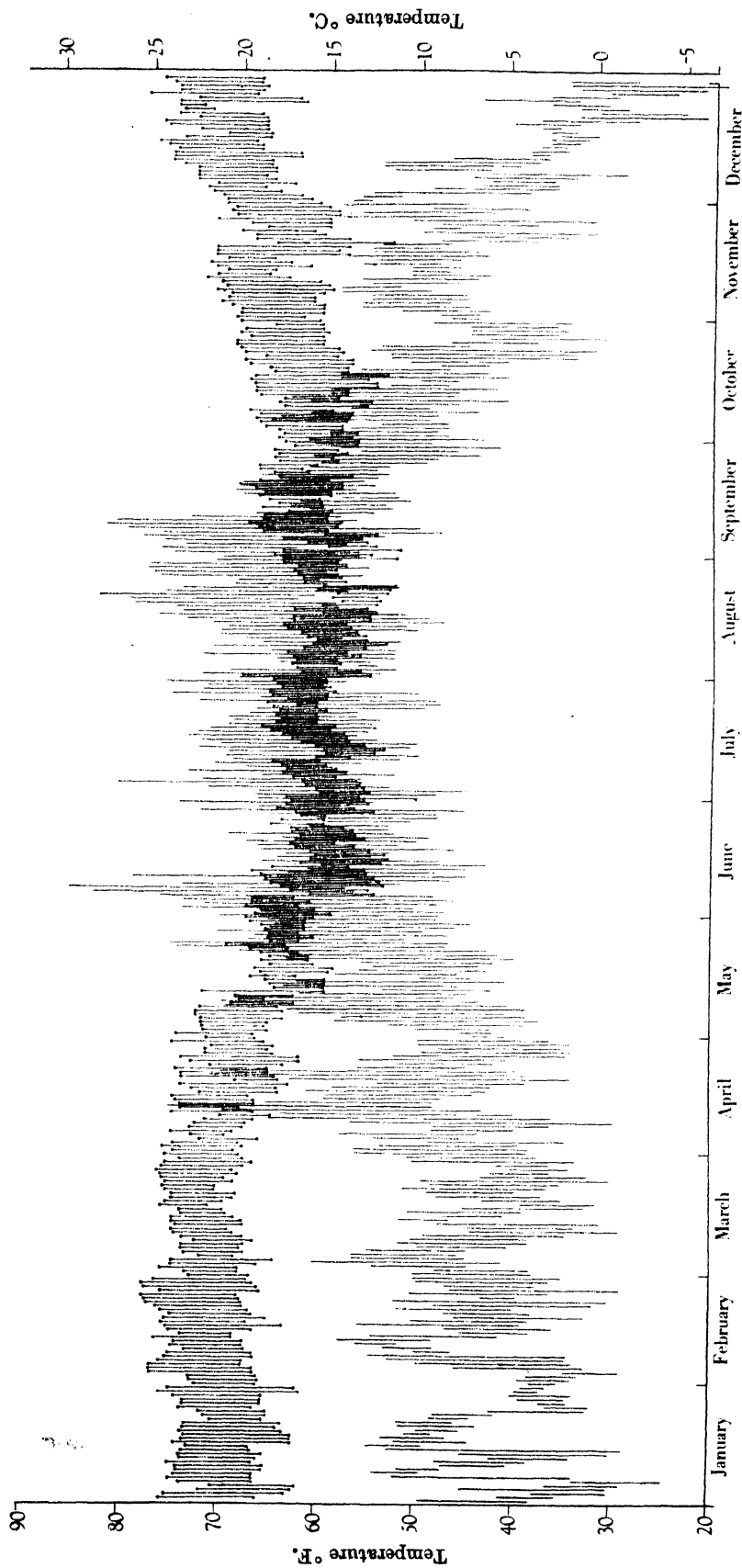


Fig. 2. Maximum and minimum temperatures for every day of the year 1939, inside the upland climax forest of Mauritius, pinheaded lines, and at London plain lines.



cols. 4, 5, 6 and 7; and the 'degree of wetness' (see below) of the exposed station, col. 8.

The mean annual rainfall over the upland climax forest is of the order of 3175 mm. (125 in.) frequently varying by  $\pm 750$  mm. The nearest site where records are available over a long period is at Curepipe Gardens where a mean of 48 years gives a value of 3130 mm. (123.3 in.). The higher value of 3791.9 mm. attributed to this station by Vaughan & Wiehe (1939) was for a period of only 5 years. The rainfall recorded at the exposed station was 3094.3 mm. (118 in.) for the year 1939, the corresponding value for Curepipe Gardens being 3498 mm. (137.7 in.). It will be noted that two maxima occur in the annual distribution of rain. This is typical of the upland rainfall as a whole, the higher maximum being due to the heavy summer rains and the second smaller maximum to the orographic or altitudinal rains of the winter months.

Table 2. *Rainfall and relative humidity at exposed station A and forest station B for the year 1939*

	Relative humidity (diff.)			Rainfall (mm.)				Degree of wetness*
	A (1)	B (2)	B - A (3)	A (4)	B (5)	B (6)	B (7)	
January	77	93	16	213.3	180.9	117.9	174.2	15.8
February	81	93	12	325.9	385.2	153.4	269.3	21.0
March	86	95	9	490.0	413.5	306.4	397.1	41.1
April	84	93	9	273.5	190.2	156.0	214.8	24.6
May	88	91	3	205.7	102.1	107.5	129.8	15.9
June	89	91	2	134.1	113.3	70.7	87.2	8.1
July	86	92	6	261.3	143.5	153.5	167.4	17.7
August	91	94	3	232.6	164.1	138.3	170.3	18.8
September	90	93	3	240.2	134.6	133.9	180.5	15.2
October	84	92	8	139.9	91.5	72.6	111.5	9.0
November	81	91	10	99.8	82.2	69.2	75.7	4.7
December	83	90	7	478.0	373.9	265.8	358.0	24.7
Sums	—	—	—	3094.3	2375.0	1745.2	2335.8	—
Means	85	92	7	—	—	—	—	—

$$* \text{Degree of Wetness} = \text{Rainfall (cm.)} \times \frac{\text{No. of rainy days}}{\text{Days in month}}$$

*Number of days with measurable precipitation* 248.

*Highest rainfall* 259 mm. in 2 days (16-17 Dec.).

The annual distribution of rain may be expressed in terms of the 'seasonal index' used by Baker and Harrison (1936) in a study of the climate of Hog Harbour, New Hebrides, where the seasonal index of rainfall is defined as the number of times the wettest month is wetter than the driest. This value is usually high in the tropics. In Mauritius the seasonal index in the lowlands is nearly seven, but in the uplands falls to five owing to altitudinal rains.

Another important factor which must affect the metabolism of the living organism is the intensity of rainfall from day to day. A knowledge of this distribution would enable a better appraisal of the real wetness or dryness of the site to be made which is impossible from the ordinary figures of monthly rainfall. Walter (1910) has suggested the use of an arbitrary figure obtained by multiplying the ratio of the number of rainy days to number of days in the month by the monthly rainfall. This he calls the 'degree of wetness' and the values so calculated for the exposed station are given in Table 2, col. 8. It will be noticed that the rainfall for March and December is practically the same, but the degree of wetness

is much lower in December owing to the concentration of the rain in this month over a few days when cyclonic conditions prevailed.

Long periods of consecutive rain or dry weather are also of interest. During the year April 1939–March 1940, there were eight occasions on which rain fell over the forest for 10 consecutive days or more. These occurred in April (12 and 15 days), May (10), August (12), September–October (19), February (17), February–March (16) and March (11). Only one dry period of more than 10 days occurred; this was in November (11 days). If the very small traces of rain which are occasionally experienced are ignored, the longest probable period without rain on the upland plateau is 15–16 days.

The rainfall measured by the three rain gauges set up on the forest floor is given in Table 2, cols. 5, 6 and 7. It is evident that the rain directly reaching the forest floor must be very variable and considerably less than that falling on the canopy owing to evapora-

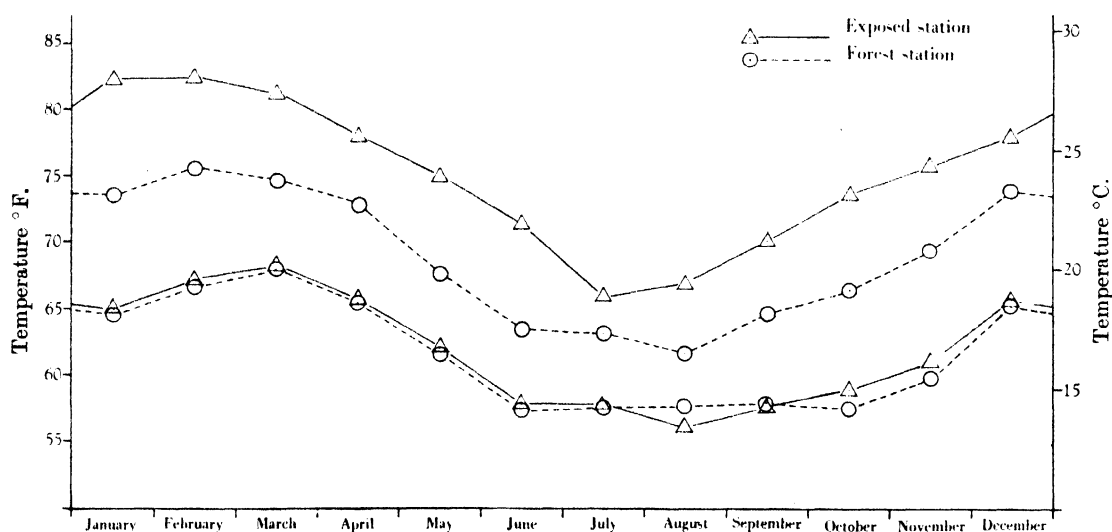


Fig. 3. Mean maximum and minimum temperatures for each month during the year 1939. Forest station, circles; exposed station, triangles.

tion from the leaves as it percolates through the different strata. The direct rainfall recorded on the forest floor was found to be about two-thirds the total experienced by the exposed station. As a general rule any rainfall of 0.5 mm. or less was not recorded by the forest rain gauges, though some showers were so local in character that rain was recorded in the forest when none had fallen at the exposed station. It was observed that the ratio of rain received on the forest floor to that measured outside the forest varies with the season; in the winter it is lower than the summer, in other words relatively more rain reaches the forest floor during the warm months of heavy downpours than in the cooler months when the rain is less heavy and the wind velocity higher.

#### *Relative humidity*

The recordings of relative humidity for the two stations are shown in Table 2, cols. 1, 2 and 3. The humidity over the whole island is characterized by the high percentage of saturation and the small amplitude in diurnal and monthly variation; these factors are, of course, accentuated inside the forest.

The mean relative humidity inside the forest for the year 1939 as measured by wet and dry bulb thermometer was 92% of saturation compared with 85% for the exposed station. The mean value on the plateau for Curepipe Gardens is 86.6%. The degree of saturation obtained for the interior of the forest is thus comparable with the figure of 95% obtained by Shreve (1914) in the Blue Mountain forests of Jamaica. The variation of relative humidity from month to month in the forest was very slight and did not exceed 5% of saturation for the whole year, whereas the variation at the exposed station was 14% of saturation. It was noted that the difference between the values obtained at the two stations was greater during the summer months.

Before passing to the daily march of humidity in the forest some points of interest concerning the general diurnal range of humidity must be considered. According to Herchenroder (1938), the degree of humidity seldom shows departures from the normal which are greater than 10% of saturation; further, these divergences on any one day have never been found to exceed 20% of saturation in excess or deficit of the normal value. The mean monthly diurnal range of humidity in percentage of saturation at the Royal Alfred Observatory, Pamplemousses, altitude 55 m. (180 ft.), is given hereunder.

Month	...	...	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean diurnal range			23.6	20.3	19.4	19.1	20.3	21.5	22.2	24.6	29.3	30.7	31.4	28.3	24.1

In conformity with the rainfall, the diurnal range is seen to reach a minimum towards the end of the summer and rises to a maximum during the comparatively dry months of October and November. As the altitude increases, the diurnal range becomes less and as soon as the forest is entered, an extremely sudden fall in range is experienced. This very significant change is best illustrated by comparing the number of days in the year on which the diurnal range fell within certain arbitrary limits. The following figures were obtained from the hair hygrograph charts recorded in the forest and at the Royal College, Curepipe, on the plateau.

Diurnal range of humidity	5% and under	5-10%	10-20%	20-30%	30-40%
Forest Station	236	75	41	10	3
Curepipe	31	65	145	107	17

For two-thirds of the year a diurnal range of only 5% of saturation or under was recorded in the forest, whereas the peak value outside the forest was between 10-20% of saturation. On 98 days of the year no variation in humidity occurred during the day at the forest station; in the same period there were 14 days of constant humidity on the plateau. The maximum diurnal range recorded in the forest was 32% of saturation.

Some interesting stretches of almost constant humidity over a number of days took place on several occasions. One of these occurred in February 1940. During the 4th of this month, no change was perceptible; on the 5th a small upward trend of 3-4% of saturation occurred in the afternoon with a much smaller variation the following day; from the 7th to the 12th onwards no daily fluctuations were observed though a steady fall of 2% of saturation took place; from the 12th to the 19th minor movements of less than 4% of saturation were observed for a few hours in the middle of each day and from then on to the end of the month another period of constant humidity set in. During the month of February rain fell over the forest every day except on 3 days in the middle of the month corresponding to the minor fluctuations of humidity referred to above. Similar conditions occurred in July 1939, when a constant humidity was registered from the 1st to the 15th

broken on 1 day by a small variation of 3% of saturation for some hours during daylight on the 9th.

The diurnal change of relative humidity, as registered by the hygrograph at the exposed station, or at Curepipe, shows that when the range is large enough the daily curve assumes a definite shape and three distinct phases may be observed which can be correlated with similar phases in the twenty-four hour temperature cycle described above. During the night the relative humidity is almost constant and at its maximum value. Soon after sunrise a rapid fall takes place in unison with the rise of temperature. The minimum is reached at 13.00–14.00 hr., after which the curve steeply ascends during the afternoon. During daylight rapid oscillations of the curve are frequent, and when the diurnal range is small the characteristic sweep of this curve is often masked by a number of small irregular movements during the day.

In the forest it was noticed that the morning decrease in humidity took place about 1 hr. later than at the exposed station and that the maximum humidity was reached rather earlier in the afternoon.

#### SUMMARY AND CONCLUSIONS

The internal climatic conditions of the upland climax forest have been studied, and data for temperature, rainfall and humidity obtained for sites inside the forest and at an exposed station nearby. The mean monthly range of temperature in the forest was only 7.4° F. during the year, little more than half the value observed for the normal climate. Screen mean minima for the month were nearly the same at both stations but the maxima in the forest were always about 6.0° F. below the exposed station. It should be noted that there is close agreement between these values and those obtained for other tropical forests in widely separated localities. Measurements of rainfall indicated that about two-thirds of the total rain falling on the canopy directly reached the forest floor. The most striking feature of the internal climate is the high and remarkably constant relative humidity, the daily range of which did not exceed 5% of saturation for the greater part of the year. The significance of the temperature and relative humidity thermo-hygrograph curves are discussed in relation to the comparative diurnal changes of temperature and humidity inside and outside the forest.

The climatic conditions described above are probably confined to a narrow zone extending from the forest floor to a height of about 3–4 m. (12–15 ft.), above which a rapid grading off to the temperature and humidity of the outside air takes place. This stable and uniform atmosphere, so different from the normal climate, combined with the stillness of the air and the low light intensity might be expected to produce some interesting adaptations in organisms which thrive in this special and restricted habitat.

The plant life living in this zone includes the sparse ground flora and the shade loving epiphytes as well as the seedlings of plants belonging to higher strata which pass a considerable period of their young life in an atmosphere very different from that which they will experience when mature.

Little is known as yet about the leaf anatomy of these plants, or of the seasonability of flowering or foliation, though Shreve (*loc. cit.*) has studied the transpiration rate of rain-forest plants in Jamaica and measured the retardation which takes place under high humidity. An examination of the external leaf morphology gives the impression of very great diversity of form, texture and colouration, even within the same species and allusion

has already been made to this notable feature of the ground vegetation. This is well exemplified by the Orchids, which range from large gregarious clumps of *Phajus* and *Calanthe* to the creeping *Goodyera* with distant papery yellow leaves, and dwarf solitary species of *Disperis* with a single pair of small purple-tinted leaves. Filmy ferns and large thick leaved *Elaphoglossum* grow side by side at the base of trees, and species of *Badula* and *Eugenia* with rigid leathery leaves often exceeding a foot in length creep over the floor of the forest intermingling with delicate pale green or pink-tinged Urticaceae.

This great range of leaf form and texture is the consequence of the humid and unvarying climate, for under these conditions transpiration proceeds at a leisurely *tempo* and there is no possibility at any time of the year of dangerous temperature or humidity gradients disturbing the metabolic processes in the leaf. Much greater latitude in leaf architecture and morphology is therefore possible than in localities where the leaf is subjected to more rigorous conditions and sudden fluctuations of large amplitude in temperature and humidity.

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# ECOLOGICAL HISTORY OF THE ENGLISH LAKE DISTRICT

By W. H. PEARSALL AND W. PENNINGTON (MRS T. G. TUTIN)

*(With two Figures in the Text)*

## ARCHAEOLOGICAL BACKGROUND

It is becoming more and more evident that any attempt to consider the British vegetation in terms of its environment can only do so against a background of human history. It is conceivable that the ideal method of studying this background, were the evidence available, might be to investigate, first, areas in which, from isolation or from other cause, the human history was simple and in which there was, therefore, a reasonable chance of estimating the direct effects of man's activities on the vegetation.

The following attempt to deal with the archaeological background of the English Lake District is justified, partly because it presents these elements of simplicity, partly because it presents most interesting contrasts with other parts of Northern England, and partly because investigations are in progress (Pennington, 1943 and unpublished) which require a consideration of this sequence of events. The treatment is limited to the Lake District proper, the high hills of Ordovician, Silurian and granitic rocks lying west of the Penrith-Shap-Kendal road. As W. G. Collingwood (1925) uses the term—it lies within a circle of 15 miles radius with Easedale Tarn (just west of Grasmere) as the centre. This is convenient because it excludes the drift-covered lowlands of Cartmel, Low Furness and West Cumberland, which have had both a different history and a different vegetation. The area thus defined as the Lake District proper was, archaeologically, not only part of the Highland zone in Britain, a zone known to have had a less varied history than the southern counties, for example, but it was also isolated from the rest of this zone by its position, by the great 'mosses' of the Winster and Leven estuaries and by the lakes of Windermere and Ullswater (see Fig. 1). Its contacts with the rest of the Highland zone lay over the Shap Fells and through the upper Eden valley, via Stainmoor. It thus followed that the eastern part of the Lake District was named from the adjacent uplands and Yorkshire, and became Westmorland.

The following account of Lake District archaeology is based upon the works of W. G. Collingwood (1925) and R. G. Collingwood (1933) who have respectively led the way in the collection and interpretation of the material. The evidence is convincing that the first human colonists of the district came from the south-west by sea. They were representatives of the 'megalithic' peoples and were responsible for the numerous stone circles and associated stone axes found near Black Combe in south-west Cumberland. They were evidently at first confined to the lowlands along the coast and are supposed to have been forest dwellers, living in temporary structures and perhaps cultivating small clearings. The provisional date of their entry is c. 1800 B.C. perhaps rather late in the tide of invasion. Other stone circles of generally similar type are found inland (e.g. at Keswick) along the route via Bassenthwaite from the upper Eden valley. All these circles are, however, more elaborate and they show additional constructional features indicating that

they are probably of a later date. Here too, round the upper Eden valley, there is said to be evidence of some fusion of cultures with 'beaker' peoples, who would be approximately contemporaneous and who would arrive via the Stainmoor gap from Yorkshire.

Strictly speaking, these early megalithic peoples were mostly outside the Lake District proper (as defined above). They centred principally in the foot-hills of south-west Cumberland. The later prehistoric remains differ in being distributed among the hills,

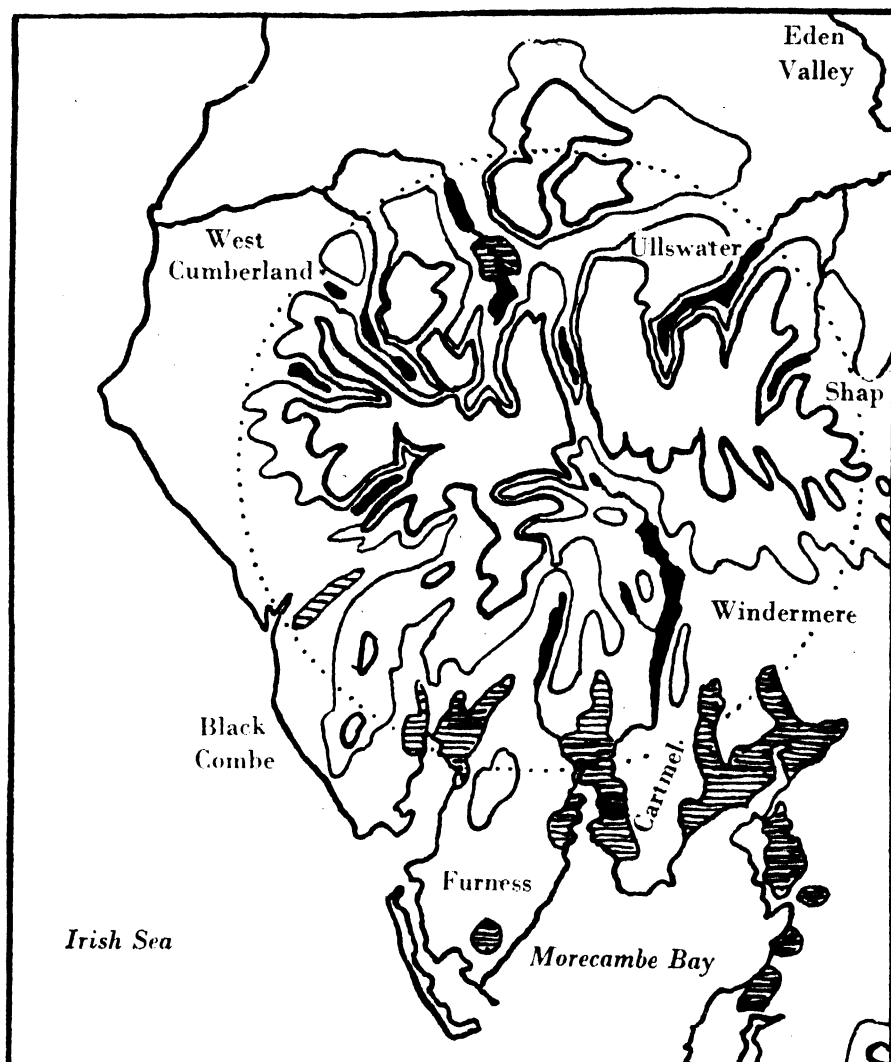


Fig. 1. Diagrammatic map of the English Lake District showing 700 and 1500 ft. (230 and 493 m.) contours, lakes in black and extensive peat-bogs shaded.

though except for isolated implements presumably dropped by hunters or travellers, they are commonly absent from the highest central areas. It seems probable that the habits of the later peoples gradually changed and that, in addition to a partial or complete desertion of the areas round the stone circles, they had evolved a mode of life in which access to the hills played an important part. At any rate, the characteristic archaeological feature of the Lake District is the wealth of tumuli, burials and settlement sites between 700 and 1500 ft. (230–490 m.). The most numerous sites are still those in the original

south-west and north-east areas, though they now show a much wider distribution. We may perhaps take the view here that they show evidence of a people gradually developing a mode of life suitable to the district. For if the Lake District in any way resembled what we can construct from existing vegetation types, it must have consisted mainly of oak woods of various types merging upwards into *Festuca-Agrostis* grasslands. The valley bottoms were undoubtedly mainly swampy alder woods, interspersed at intervals with equally impassable willow carrs and developing 'mosses'. The logical mode of life in such an area for people without metal cutting-tools would no doubt include fishing in the tarns, hunting in the woods and grazing sheep and cattle along the upper and more open edges of the woodlands and on the grasslands. The distribution of the archaeological remains seems to offer conclusive evidence that the upper zones (presumably open woodland or grassland) were the areas occupied and there is, moreover, one very suggestive fact which seems to relate human occupation to the upper tree limit. In the central and eastern Lake District, the present woodland remains extend to at least 1500 ft. (457 m.) and plantations have been made even higher. In the west, *per contra*, on slopes facing the Irish Sea, the existing tree limit is low, probably not more than 600 ft. (182 m.), though formerly, when the adjacent lowlands were tree-covered, the upper limit of woodland could no doubt have extended much higher. A precisely similar variation in altitude is shown by the prehistoric remains in the two areas; those of the western margins are almost always at a lower level (400–700 ft.) than those of the centre and east (800–1000 ft.) and the actual altitudes are suggestive of a people living along the woodland margins.

Now as to the archaeological relations of the remains, it seems that the tumuli and burials are, on the whole, of Neolithic-Bronze Age types (usually showing cremation) though, as they may include bodies in a straight position, there are probably also examples of 'British' type. The few cultural objects associated with the burials are Neolithic in affinity, metal being unknown. Such of the settlement sites as have been investigated are of a later age. They may show clear traces of occupation in Roman time and they are considered to be generally of Romano-British date though of Neolithic culture. R. G. Collingwood therefore suggests that the Neolithic peoples persisted in the hills, only gradually acquiring materials and customs from outside, and remaining practically unchanged until Roman times or later.

In these circumstances, it seems that we can only say that after the preliminary period of colonization of the coastal and lower lands, there was a period of settlement and of establishment in the hills which, judging by the tumuli was probably well developed by 1000 B.C. At some later time, presumably after this, the practice of building stone huts developed, so that later the existence of a quite considerable population can be assumed in certain areas. Some at least of these were probably occupied in Roman times, say A.D. 300. Thus we may perhaps imagine the hill peoples on the whole slowly increasing in numbers until the Romans came, after which the rival attractions of Roman settlements or service might possibly have caused a decline.

It should perhaps be emphasized that Bronze and Iron Age implements and materials are practically unknown in the Lake District proper. Even the Roman influence was of the slightest. The hut sites of this period that have been examined show a few potsherds at most for dating purposes and it is quite clear that the people must have been at the vanishing point of Romanization. On the other hand, they seem to have been numerous and the construction of the Roman road along the summit of the High Street range, not



only served as the shortest and probably driest route to the north, but apparently it also passed near to the bulk of the eastern population and thus no doubt had a military value. This and the other Roman road in the Lake District, the lateral one going west from Ambleside to the Ravenglass port, were both primarily strategic and part of the western defences of Hadrian's Wall. Ambleside seems to have been the only much occupied site on either road, and it was evidently of the frontier station type. No doubt its inhabitants cleared a good deal of timber in the vicinity for fuel and probably some of the valley alder woods in Little Langdale were also cleared away from the immediate neighbourhood of the road.

If Roman influence in the Lake District was small, that of the Anglians was non-existent. The Anglian farmers were not attracted. A few farms on the drift-covered lowlands of Low Furness and a colony in the lower Eden valley (*Englewode* or *Anglewode* = Inglewood) by invasion through the Tyne gap can be traced but there is nothing to represent this phase in the Lake District proper. Consequently, between the collapse of the Roman province and the coming of the Norse c. A.D. 900 there is nothing significant except a number of high level 'British' forts which probably date from after the Roman occupation. They are practically absent in the southern half of the district, so that they point to attack from the north—presumably from the Picts (from Scotland) and the Scots (from Ireland). It seems certain that the British persisted in the hills and that they were there long after the Norse land-takes of the tenth century. The evidence is mainly that of the Norse place-names. When history came to be written, the High Street road was *Brette-strete*, the 'British' road, the Barnsear settlement (south of Eskdale) is Birkby, known to be a corruption of 'Breteby', the '—by' of the British. Often a Celtic name is associated with a Norse affix—showing that the Norse maintained some at least of the native inhabitants to assist them. More striking still is the retention of names of Celtic origin in the numerals traditionally used until recent years for counting sheep.

The early history of the Lake District proper is thus of extreme simplicity. As R. G. Collingwood (1933) has emphasized the culture of the population remained at a Neolithic level even after the Roman period. Two changes only are apparent in the long interval after colonization. First, the tendency towards the occupation of upland sites, which may have been developed by about 1000 B.C. and secondly, the development of a technique of building huts with walls of stone rather than of perishable materials, which method was evidently developed by about the beginning of the Christian era.

The development of an upland population was natural in the Lake District, not only because the early open spaces were the high-level grasslands, but also because the higher mature woods tend to approximate to pure oak stands—with no subordinate shrub layer. Freedom of movement through these woods is often nearly as great as if trees were absent. This type of wood is characteristic of shallow slaty soils and must formerly have been of very wide distribution. In contrast the valley bottoms must have been mainly alder woods or willow carrs—merging into damp oakwoods with a tendency towards a considerable shrub development (e.g. *Corylus*), and probably a high ash content. It is perhaps doubtful if many woods of this type now remain—but fragments on alluvial gravels or on wet screes or flushes are nearly as impenetrable as alder-willow woods. Whatever might be the case elsewhere, it seems probable that primitive settlers in the Lake District would tend to congregate on the middle slopes, where drainage would be good and there would be easy access to the upper grasslands. It may, in passing, be noted that they avoided

the thinnest soils and rocky knolls. From an ecological point of view this occupancy would have two effects, it would first intensify the proportion of grasses in the woodland ground flora (see Pearsall, 1936) and, secondly, by the constant destruction of seedlings, it would prevent the natural regeneration of trees.

It should be noticed also that two other processes of ecological importance must have been in continuous operation. First, the continuous removal from the soil, by rain-wash, of soluble minerals, and particularly of bases like lime and potash, resulting in the development of base-deficient soils that finally become extremely acid. Secondly, on many of the higher hills there are areas of slight slope, which tend to remain water-logged and to develop base-deficient peat. On many Lake District hillsides, these little bogs have tended to 'spill over' and to affect the soils and vegetation below them. The two tendencies would be often complementary and there can be no doubt that many areas within the original woodland zone, would not now support natural woodlands easily owing to their base-deficient or boggy character. It seems logical to suppose that these factors were tending to depress the tree limit even before the original human colonizers appeared, and that there must then, as there are now, have been considerable tension zones in which woodland or scrub could just maintain itself in spite of adverse edaphic conditions, but in which any additionally adverse influence such as grazing would be decisive in preventing regeneration. These sensitive zones would then, as they do to-day, tend to lie along the upper margin of the oakwoods.

The second main phase of Lake District exploitation followed the Norse land-takes, c. A.D. 900-1000. These started in and progressed up the valleys, and they followed a constant form which can be readily traced from the place-name evidence (see W. G. Collingwood, 1925). The 'by' near the valley entrance was associated with summer farms (*saeters*) and clearings (*thwaites*) further up the valley, while in almost every valley swine rooted in the more distant woods (Grisedale, Grasmere and Swinside, etc.). While the new feature in human influence was the extensive valley clearance which resulted, it has been suggested also that the Norse colonists, coming from another mountainous country, had a mode of life based very largely on sheep. They used the milk of the ewes for their dairies and the wool for their clothes. An important result of the new era of exploitation, therefore, would be an intensification of sheep-grazing as a result of the increased population. This tendency was not eased as time went on, for when the Lake District emerges into written history in the thirteenth century, we see that the most prominent feature of the Norman system is the exploitation of the hill country by the great Cistercian Abbeys (Furness, Bylands and Calder, in particular). This involved not merely the existence of flocks of sheep adequate to maintain the local population, but their multiplication on a scale sufficient to build up and support the vast export trade of wool handled by the Cistercian Abbeys. It has been shown that even the large flocks maintained by the northern abbeys themselves, were quite insufficient to account for the volume of this trade. The monks must also have been merchants on a very large scale, and their activities in this respect must have tended to increase the flocks of the whole of the sheep-raising population.

To a lesser extent, the numerous bloomeries developed in this district must also have reduced very greatly the available woodland. By the middle of the sixteenth century (A.D. 1556) it was necessary to enact that the smelting of iron be discontinued in order to prevent further woodland destruction and, although in a short time, the bloomeries seem

to have been as vigorous as ever, by 1700 the largest forges removed to Bunawe in the Western Highlands, because it was no longer possible to obtain charcoal in the Lake District. We may conclude, and there are many incidental facts in support of the conclusion, that deforestation had reached its greatest extent during the period 1600–1700.

It is perhaps fortunate that the last 150 years have seen a growth of romantic interest in the Lake District accompanied by large-scale amenity planting and woodland conservation, which has on the whole followed natural patterns. Thus the Lake District as we see it to-day is a much more heavily wooded region than it was 200 years ago. It is, however, still primarily a region of extensive mountain sheep-walks and of small valley grazing farms, the latter utilizing almost all the areas of deep or alluvial soils of moderate fertility. And it is well to remember that the bottom of every valley, meadow and pasture is riddled with drains and is only maintained in a useful state by constant liming and draining to keep down the ever-encroaching moss.

Against this background of history, we must consider other new lines of evidence derived from the study of the bottom muds in Windermere. The evidence is of two sorts: first, that dealing with the pollen analyses, and secondly, data concerning the organic content of the mud. The pollen records for the lake mud have proved of interest mainly because of their record of late glacial conditions (Pennington, 1943–5). In the post-glacial muds, pollen grains are rather scarce and some caution must consequently be exercised in interpreting any changes in the proportions of different types.

Taking the records for a fairly representative deep-water section (4210 at 46 m. outside Low Wray Bay) as given in Fig. 2 we note that one very definite sign of changes in pollen proportions is evident from 0.5 m. to the surface. This part of the core shows a general reduction in alder and in hazel pollens with corresponding increases in pine pollen and in grass-sedge pollen. Adopting the provisional time-scale of Pennington (1943) the initial depth, 0.5 m., corresponds to an approximate date of A.D. 1200 and the changes are well marked by 0.4 m.—equivalent to about A.D. 1400.

It seems probable that we have here clear evidence of:

- (a) The clearing of the valley alder swamps by the Norse.
- (b) The destruction of low-level oak woods with the hazel.
- (c) The great extension of grasslands resulting from this destruction and from sheep-walk exploitation by the abbeyes.
- (d) An extension of pine along the partly drained ‘mosses’ and later by planting.

Thus the pollen record exactly fits the historical record.

It may next be noted that certain other pollen changes are noticeable at an earlier stage. At about 1.75 m. in this core, pine disappears and there is subsequent general rise in grass-sedge pollen. Our suggestion would be that the disappearance of pine pollen marked the final destruction of the original high level open pine-heath woods, and it might be expected that a corresponding increase in grass-sedges would follow—whether these open pine heaths were converted into grassland by grazing or changed towards ‘moss’ vegetation. The latter change might result from degeneration of drainage following the downward extension of ‘moss’ influence and the progressive extension of soil leaching. It may be noted that a marked decrease in hazel, a plant of base-rich soils, had taken place earlier (after 2.25 m.). The approximate dates of these events on the time scale are 2000 B.C. (2.25 m.) and 1000 B.C. (1.75 m.).

It seems an open question, how we should interpret these facts. It would be possible

to suggest that they might represent the effects of the earliest inhabitants in clearing the upper pine heaths and hazel scrubs, though the absence of a considerable rise of grass-sedge pollen seems to tell against this interpretation. On the other hand, the effects of progressive leaching should have been pronounced by this time, and they also would lead to final degeneration of high hazel scrubs and later perhaps, to 'drowning' of the open pine heaths. After 1100 B.C. when the pine finally disappeared, there was a considerable upland population (see p. 139) marked in the pollen records by a considerable rise in grass-sedge pollen, as well as by disappearance of pine. It is intriguing to speculate as to whether the rise in grass-sedge pollen at 1 m. and its fall at 0.8 m. are significant. The former

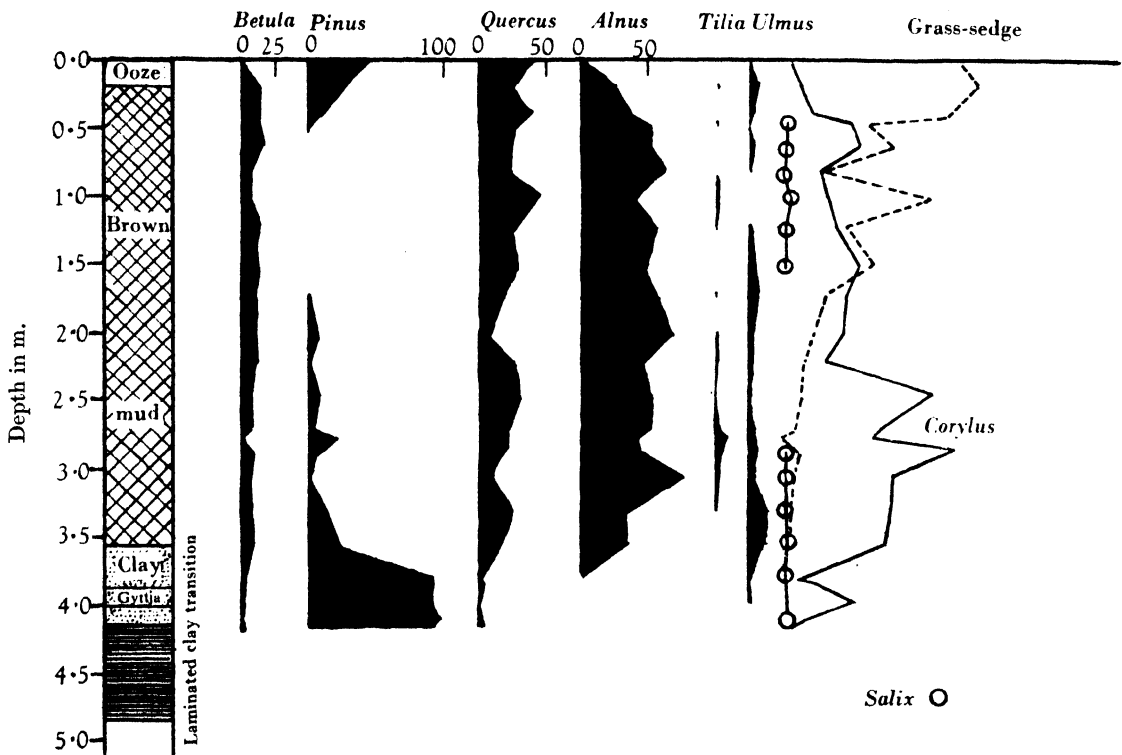


Fig. 2. Showing pollen proportions as percentages of tree pollen in a typical Windermere deep-water mud-bore.

represents about A.D. 250—a period when there was a large upland population—and the latter (0.8 m.) represents about A.D. 650—the middle of the Dark Ages and possibly of a wetter climate.

Whether these are significant features or not, it is clear that the pollen diagrams faithfully reflect the two main features of human history in this district, the invasion and upland settlements of Neolithic man and the Norse settlements of the last 1000 years.

The data for changes in the organic content of the lake muds are equally of interest against this background. Two sets of estimates are included in Table 1. The estimates are for total nitrogen (N) and total carbon (C), the former being estimated by the micro-Kjeldahl method and the latter being obtained either by wet combustion or estimated as half the loss on ignition. The loss on ignition might give slightly high results relatively, though in the absence of appreciable amounts of carbonates it is not likely to introduce

any serious alteration of the conclusions drawn here. A reduction of the loss on ignition estimates of carbon by 1.7% is considered to be the maximum adjustment possible.

The estimates must also be considered in the light of the fact that, locally, high accretions of organic matter occur—notably about 350 cm. depth where, indeed, small wood fragments are often visible. Dead leaves are also at times embedded in the mud. We should,

Table 1. *Carbon (C) and nitrogen (N) estimations from deep-water muds obtained with Jenkin borer in Windermere*

4210 at 45 m. and J. 40. 1 at 65 m. Asterisked figures for carbon are by wet-combustion method. Depths are cm. below mud surface

		C		N		C/N
Depth class		4210	J. 40. 1	4210	J. 40. 1	
Surface ooze	0-5	9.4*	—	0.92	—	10
		12.1*	—	0.48	—	25
	8-20	7.0*	—	0.20	—	35
		—	—	0.63	—	—
		5.9*	—	0.49	—	12
		—	7.2	—	—	—
	20-29	6.3*	—	0.33	—	19
		—	—	—	0.61	—
	30-39	—	8.5	—	0.45	19
		11.7	—	0.57	—	21
	40-49	—	10.3	—	0.50	21
		—	10.75	—	0.49	22
	50-59	10.4	—	0.68	—	16
		—	10.4	—	0.58	18
	60-69	11.0	—	0.72	—	15
		—	11.05	—	0.91	12
	70-79	—	11.2	—	0.92	12
		—	12.05	—	0.87	14
	80-89	9.9	—	0.57	—	17
		—	—	—	0.71	—
	90-99	—	12.8	—	0.75	17
		—	12.2	—	—	—
	100-109	—	—	—	—	—
		—	—	—	—	—
	120-129	12.7	—	0.87	—	15
		—	—	—	0.91	—
	130-139	—	—	—	0.87	—
		—	13.6	—	—	—
	140-149	—	14.4	—	—	—
		—	—	—	—	—
	150-159	—	—	—	—	—
		—	—	—	—	—
	170-179	13.6	—	0.82	—	17
		—	—	—	—	—
	204-209	11.7	—	0.79	—	15
		—	—	—	—	—
	210-220	—	11.65	—	0.76	15
		—	—	—	—	—
	222-224	10.0*	—	0.64	—	16
		—	—	—	—	—
	240-250	—	10.5	—	0.75	14
		—	—	—	—	—
	266-271	10.0*	—	—	—	—
		—	—	—	—	—
	300-310	—	—	—	0.69	—
		—	—	—	—	—
	336-340	9.9*	—	0.58	—	17
		—	—	—	—	—
	346-351	10.5*	—	0.77	—	13
		—	—	—	—	—
	354-359	13.6	—	0.45	—	24
		—	—	—	—	—
Transition	408-414	3.2*	—	0.27	—	13
		414-418	—	—	—	—
Laminated clay	418-420	2.0*	—	—	—	—
		—	—	—	—	—
	506-511	1.35*	—	—	—	—
		0.55*	—	—	—	—

therefore, in interpretation, attach no importance to a single high or low value. Furthermore, there is evidence (Mortimer, 1942) that conditions at the mud surface are unstable and it seems probable that the surface decay will cause some loss of organic matter in the top 10 cm. The values for nitrogen are subject to much greater variability than those for carbon, simply because they are done on very small samples (10 mg.). The estimates of carbon by loss on ignition show good agreement between replicates.

Allowing for these features and excluding the basal zone of rising organic matter which corresponds to a pine-birch pollen period, we can distinguish four main zones (see Table 1) in the sediments, each characterized by fairly constant values for organic matter. The two most interesting are the zone of higher values between about 1.70 and 1.20 m. and the zone of low values between about 0.45 and 0.10 m. The zone of high organic content centres round estimated dates of about 1100–250 B.C., when the highest values occur. It will be noticed, however, that the values for high nitrogen tend to continue up to about 60 cm. in one core. The zone of lowest organic contents, from c. 0.46 m. upwards, corresponds to the modern period, A.D. 1200 onwards. The higher organic content of the black surface mud may represent a real increase in the last 100 years or so—though the organic matter here may be still decomposing.

The explanation of these results depends on the view taken of certain main possibilities. Assuming that the organic matter in a deep-water deposit represents mainly the remains of planktonic organisms, then a higher organic matter might represent either a greater rate of production of plankton (i.e. greater fertility in the lake water) or else a lower rate of accretion of inorganic sediments. The latter would imply fewer floods and hence probably a lower rainfall. It is conceivable that a lower rainfall might also lead to heavier plankton production if, for example, light conditions controlled plankton production. In the English Lake District, however, the evidence is that factors such as the concentrations of plant nutrients containing nitrogen and phosphorus are the main factors *at present* determining the amount of plankton production. These compounds are mainly the product of organic decay in the soils of the drainage system, washed out by rain into the surface waters. They would presumably tend to be present in higher concentrations in the lake water whenever humus breakdown was accentuated in the drainage system. The particular feature likely to lead to humus breakdown would be forest destruction. It should, however, also be noted that contamination of water by animal organic matter also raises its fertility in plankton production very considerably, not only because organic materials of this type are rich in nitrogen and phosphorus but also because they are very rapidly decomposed in soils and natural habitats.

Thus forest clearing and an increased population of grazing animals would both tend at first to increase fertility of the lake waters. But increased exposure of the soils in the lake drainage system would tend to increase the rate of removal of soluble substances and hence would finally lead to reduced fertility. Further, it is almost universal experience that forest clearing and humus destruction are followed by greater soil erosion. It would thus be expected that forest clearance would be succeeded in the lakes by an era of greater inorganic silt deposition. This would coincide in time with the period when the stored humus of the original forests was becoming exhausted so that the fertility to plankton of the surface waters was reaching a low ebb.

We could reach a similar conclusion more easily if the organic matter in the lake muds were considered to represent mainly organic materials, e.g. dead leaves, carried into the lake from the drainage system. In this case the amount of organic matter so carried would depend mainly on the productivity of the drainage system, and, allowing for the probability of increased soil erosion as forest clearance progressed, we might argue that the observed diminution of organic matter since 1000 B.C. was a measure of diminished soil fertility in the drainage system as a whole. In this case, however, it is not easy to see any reason for an increase in mud organic content in the zone 210–120 cm.

One of the objects of attempting to estimate both carbon and nitrogen separately in these muds was to obtain a means of deciding between possibilities of this type. The carbon-nitrogen ratio (C/N) of planktonic materials is very low, commonly about 6 (see Misra, 1938), whilst that of organic material from terrestrial vegetation is correspondingly high, between 15 and 30, though it tends to fall during the decomposition of these materials in soil to a level characteristic of the climate in which the soils exist. There is reason to believe that a similar, more or less constant level finally characterizes lake muds whatever the source of the original organic matter. In actual fact, the C/N ratio of the organic matter in the Windermere muds seems to vary rather constantly about 16, a value possibly suggesting, if the conclusions in the last paragraph are ignored, that this organic matter is derived primarily either from terrestrial vegetation (e.g. dead leaves) or from emergent aquatic vegetation. The latter possibility is not likely to be important in Windermere.

In one zone, however, between 50 and 10 cm., the C/N ratios do show a tendency to be higher, for out of the seven actual estimates, six give values of 19 or more. This suggests either that the planktonic component of the mud was much reduced at this time or that the source of terrestrial material had changed to one with a higher C/N ratio, e.g. grass leaves instead of tree leaves or perhaps even oak leaves, for example, rather than alder or hazel leaves. On the whole, however, in the English Lakes, Misra (1938) found that there was not much difference between the C/N ratios of lake muds even when taken from lakes surrounded by very different sorts of vegetation. The more obvious correlation was that lakes with a higher plankton production tended to have mud with lower C/N ratios. For this reason we suggest as more probable, the assumption that the zone of low organic content at 50–10 cm., was also a zone of low plankton productivity.

The three high nitrogen values in the second series of estimates (J. 40. 1) between 60–90 cm., suggest a period of high plankton production at that time. Because of the absence of confirmation, either from the corresponding carbon values or from the other core, opinions on their significance should perhaps be reserved for the present. Note for example the difference between the samples at 60–69 cm.

It seems from this discussion that on *a priori* grounds alone, it is more probable that the changing organic content of the Windermere sediments represents the events that would follow naturally from the exploitation of the forests and the depression of the tree limit and it seems to be rather less probable that it is associated with climatic changes. Whatever may be the real explanation and this may, of course, include both factors, it is noteworthy that the changes in the sediments follow the historical pattern very closely. If the megalithic peoples entered the country about 1800 B.C. and there was a large population in the hills from 1000 B.C. on, the first period of primary exploitation would correspond closely with that of maximum lake fertility (say about 1100–250 B.C.). The exploitation of the district would not be further continued until the arrival of the Norse, for their colonization (say A.D. 1000 onwards) extended it to the lower valleys. This secondary exploitation would be further emphasized by the policy of the Cistercian monks in exploiting sheep walks and, to a lesser degree, in promoting ore-smelting. So it seems significant that about the time (A.D. 1550–1600) the minimum of lake fertility seems to have been reached, we should get a Royal order (A.D. 1566) suppressing the bloomeries in order to prevent any further destruction of woodland in the district with which we are dealing. Even the higher organic content of the most recent muds agrees with the

recent development of a much greater population in the district and an increase in lake fertility as a result of sewage affluents, although, as we have already suggested, too great an emphasis cannot be placed on this apparent correlation, until we know what proportion of the organic matter is lost in the decay of the uppermost layers.

We do not wish to deny the possibility that climatic changes may have had some influence in bringing about these events, for we observe that the beginning of the period of the Neolithic colonists apparently coincides in the deep-water sediments with a fact for which no other simple explanation can be readily advanced. This is the final disappearance of *Melosira arenaria* var. *hungarica*, a diatom that had been extremely abundant in the immediate post-glacial period and one that may consequently require conditions of low temperature. Parallel to this is the fact, possibly less significant, that a common diatom in the deposits, *Gomphonema geminatum*, shows a temporary phase of maximum abundance at the same mud level (2.0 m.).

It should, we think, be noted also that the time scale for the Windermere muds, is a provisional one (Pennington, 1943) and that it is based on the assumption that a constant mass of inorganic silt was deposited per unit time throughout the period represented by the muds. If this were not the case, some alteration of the dates might be necessary. In practice this provisional usage has the advantage that it makes allowance for the greater compression and lower water content of the more deeply buried muds. In effect, it gives a date of about 6500 B.C. for the appearance of alder-mixed oakwood. Tage Nilsson (1935), using the Swedish geochronology, obtained a figure of 6200 B.C. for this phase in South Sweden. It seems then that the Windermere time-scale is at least of the right order of magnitude.

We could, of course, make corrections adopting as a basis another extreme, namely the assumption that the rate of *organic* sedimentation had been constant throughout the post-glacial period—represented by an average constant accretion of c. 11 % of carbon in silt. We should then imply that the rate of *inorganic* silting had been greatly accelerated in the short period represented by zone 10–50 cm. and greatly retarded ( $\times 0.83$ ) in the period represented by zone 100–180 cm. Thus the former zone would actually represent a shorter interval and the depth of 30 cm. would correspond only to A.D. 1680 or so. The next point affected, 100 cm. (and all between this and 30 cm.) would also be c. 100 years later. Hence the period of high organic content (120–180 cm.) would end about 150 B.C. but would now continue for  $850 \times 1.2$  years, that is starting at c. 1270 B.C., instead of at 1100 B.C. It will be noted that the corrections applied do not make much difference to the estimated dates and are probably well within the range of error of such estimates and certainly within that of the archaeological datings. We do not suggest that these corrections are at present desirable. The balance of probability seems to us to favour the broad interpretations put forward at an earlier stage and the employment with caution of the existing provisional scale.



## SUMMARY

This paper contains a summary of what is known of the history of the English Lake District and attempts a correlation with certain features of organic content and pollen analysis of the muds of Windermere.

There are grounds for assuming that the Windermere drainage system has passed through the following stages:

1. A late glacial and immediate post-glacial phase of rapid erosion and stabilization by vegetation (pine-birch forest).
2. A steady state of alder woods and oak forest.
3. A phase of primary (upland) occupation by man and incipient forest degeneration, with disappearance of high level pine-heaths (say 1500 B.C. to A.D. 900).
4. A period of secondary (valley) occupation (by the Norse), increased grazing and accelerated degeneration (say A.D. 900–1300) accompanied by draining of alder swamps and 'mosses'.
5. A period of economic exploitation for wool and timber (c. A.D. 1300–1750) with extreme woodland and soil degeneration.
6. Romantic period of replanting and amenity exploitation (A.D. 1750–1940).

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## RINGINGLOW BOG, NEAR SHEFFIELD

## PART I. HISTORICAL

By VERONA M. CONWAY, *Department of Botany, Sheffield University**(With eleven Figures in the Text)*

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## 1. GENERAL DESCRIPTION

A ridge of high ground separates the Derwent valley from the valleys which run eastwards towards Sheffield. A millstone grit 'edge', so characteristic of this neighbourhood, makes a bold western escarpment to the ridge, the highest part of the escarpment in this area being a hill called Stanage Edge, which rises to 1500 ft. (460 m.) and shows up conspicuously in the view from the eastern side of the ridge. In the lea of Stanage Edge lies a long area of saturated bog occupying a very shallow depression in the main plateau. Fig. 1 shows the general features of the area. The bog is cut into two by the uppermost reaches of Burbage Brook, which, with its tributaries, forms the sole drainage outlet of the bog, save for a very small and ill-defined overflow in the north-east corner, between Rud Hill and the quarries. The western half of the bog bears the name White Path Moss on the 6 in. O.S. map; the eastern half is the subject of the present study, and when 'the bog' is spoken of in this paper, it is this eastern half to which reference is made. Since it has no name on the O.S. maps, I have chosen to call it Ringinglow bog, after the nearest village, which lies a mile to the east. Fig. 1 shows that the bog lies at an altitude just over 1300 ft. (400 m.) with a very gradual surface slope down to Burbage Brook.

The peat cover is thick over the main part of the bog, though it is shallower on the sides of the basin and thins away entirely where the gritstone summits shoulder up through it. The general lay-out of the area, and the depth of peat discovered by preliminary pokings with a peat borer, suggested that somewhere there might have been a true basin in the rock surface in which topogenous peat might have accumulated. I was looking for some-

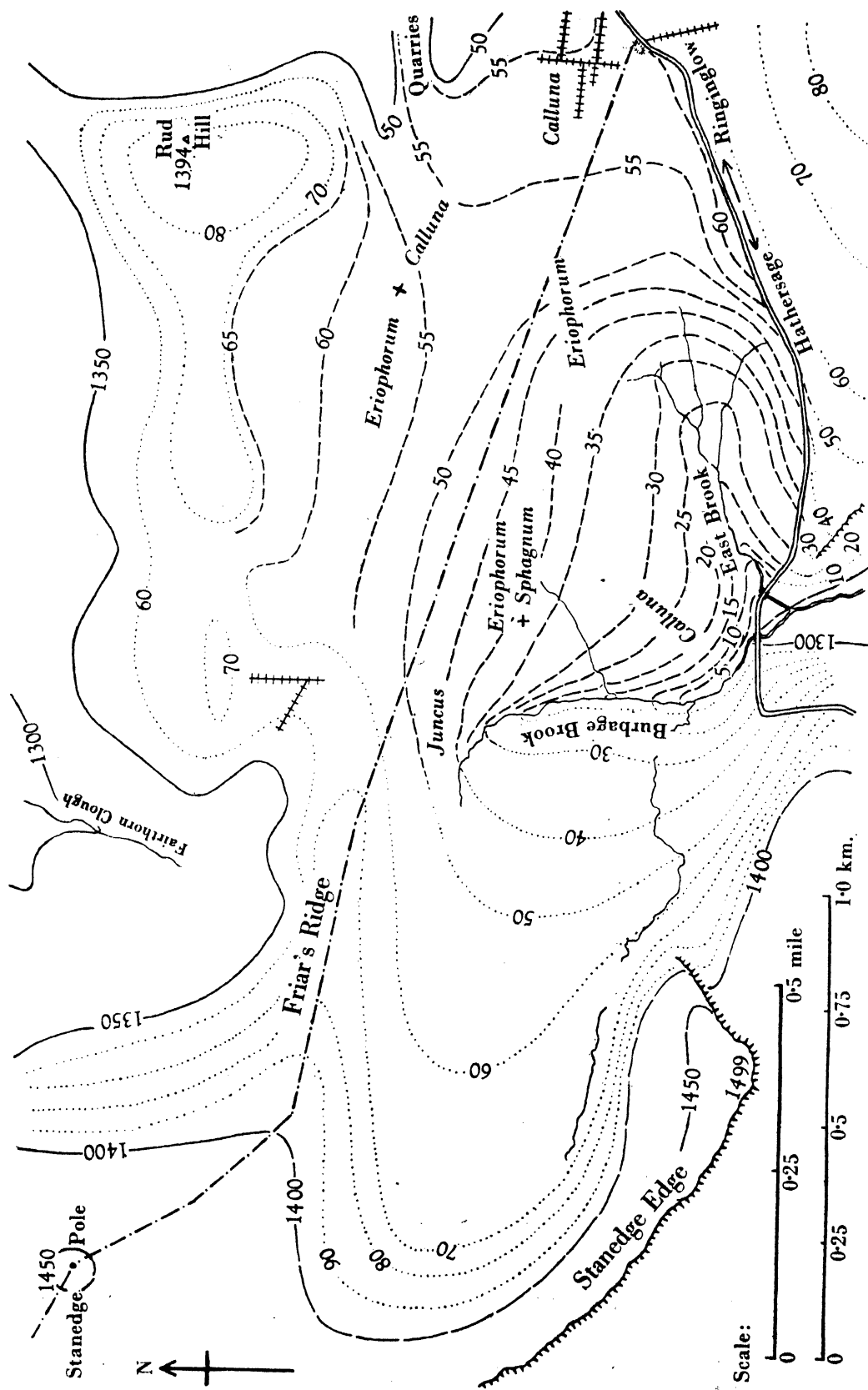


Fig. 1. General topography of the area. - - - - - County boundary: Yorks to north-east, Derbyshire to south-west. — Contours from 6 in. O.S. map. — Contours from 1 in. O.S. map. - - - - - Contours from levelling survey, in ft. above 1300 ft. .... Contours sketched in to show general relief, in ft. above 1300 ft. ++++++ Artificial drains.

thing of this sort in the southern Pennines in the hope of obtaining a long pollen diagram which should help in interpreting diagrams already obtained from blanket peats in other places in this district. The data to be described later did not, however, justify this hope, that is to say, the whole peat area must in the main be considered as blanket peat. Nevertheless, by the time this conclusion had emerged, it was clear that this was a region of considerable ecological interest, both from the point of view of historical development and of present vegetation and habitat conditions.

In strong contrast to most areas of blanket peat in the southern Pennines, Ringinglow bog is still a genuine bog in that the water table is right at the surface through most of the year. Broadly speaking, one has to seek for such a condition north of the Aire Gap, and amongst areas ecologically described in recent years, Stainmore Forest (Pearsall, 1941) springs to mind as the one most valuable to compare with Ringinglow bog. But while Stainmore Forest over a fair proportion of its area has retained the characteristic dominance of *Sphagnum* (Pearsall's Moss A type), Ringinglow bog shows quite other dominants, and even though there is a small area, indicated in Fig. 1, in which *Sphagnum* is fairly abundant, the genus is represented almost entirely by *S. recurvum*.

*Calluna vulgaris* and *Eriophorum vaginatum* are the present main dominants; the former attains complete dominance where the drainage is good enough to allow surface drying in the summer. The two areas mainly concerned are the south-west corner of the bog and a south-eastern patch surrounding the artificial drains. *Eriophorum vaginatum* is the sole dominant in what will be referred to as the central region of the bog, around site 10 (see Fig. 2), though it lies actually south-east of the geometrical centre. Elsewhere it is co-dominant with *Calluna*, or mixed with much *Eriophorum angustifolium*. *Deschampsia flexuosa* is widespread and indicates the 'derived' nature of the present surface vegetation. The communities grade into one another in a way which renders it difficult to make a satisfactory vegetation map, considering the size of the area. The one type which stands out clearly is that dominated by *Juncus effusus*; it consists essentially of a 'flush' vegetation, though it is full of interesting complexities.

Thus the bog surface is very unlike the regeneration complex characteristic of raised bogs, or the less hummocky but still *Sphagnum* dominated community which is typical of undisturbed blanket bogs such as those of Ireland and of small areas of northern Britain, as for example the Stainmore area previously mentioned. Nevertheless there is a very striking fact about Ringinglow bog, namely that one has only to go to any spot in the central region of the bog, pull up a tuft of cotton-grass, and scrape away 5 cm. of solid surface, to obtain a handful of the freshest and most typical bog-building *Sphagnum* peat, showing large well-preserved *Sphagnum* shoots, mainly of the *S. cymbifolia* types. Clearly then the degradation of the bog surface is of extremely recent origin, and several lines of evidence suggest that the *Sphagnum* dominance gave way somewhere round 100 years ago. There are still occasional tufts of *Erica tetralix*, looking unhealthy, together with a widespread though inconspicuous occurrence of *Oxycoccus quadripetalus*, and in 1942 a single specimen of *Andromeda polifolia* was found. These three species may all be considered as relicts of a former *Sphagnum* bog vegetation.

Part II of this paper will deal with the present surface vegetation and the causes of the change from a *Sphagnum* dominated community, and hence these matters have merely been glanced at here. It is perhaps worth mentioning, however, that while the change appears to be contemporaneous with and hence possibly caused by the industrial revolution,

with its attendant atmospheric pollution, I am not at present inclined to adopt the view that atmospheric pollution has been more than a minor factor in the degradation of the bog surface. This attitude is based on experience of parallel examples of degradation in many parts of north Britain far removed from industrial influences. The abrupt change, which concerns the eastern half of the bog rather than the western, can probably be explained as due to the effect of the cutting of the artificial drains at the eastern end.

The more remote history of the bog has to be investigated by more intensive methods than mere scraping at the surface, and to these methods we must now turn.

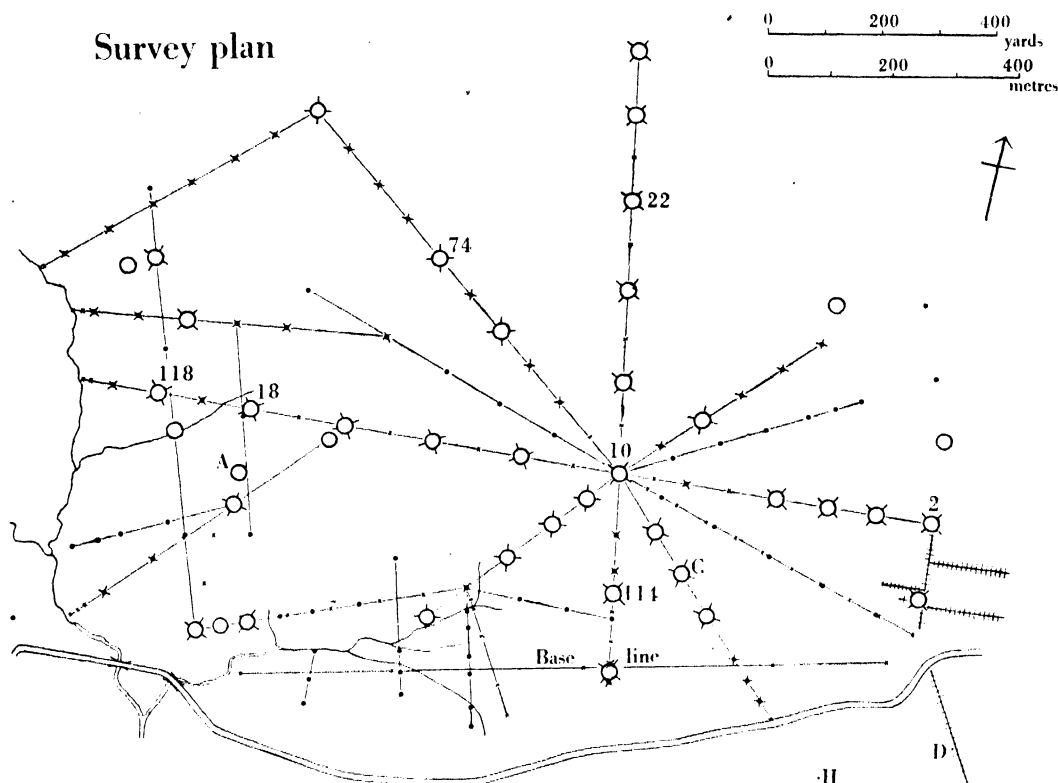


Fig. 2. Plan of boring and levelling surveys. ○ Sites where complete profiles were examined. • Sites of depth probings, with only lowest samples examined. × Sites where surface levels were read. (A number of the bore-points were left unlevelled because the levelling instrument was only available for a short time.)

## 2. BORING AND LEVELLING SURVEY

Fig. 2 presents the details of the way in which the survey was carried out. It would have been preferable to use a regular grid system for the basic lines of the survey, but this was not possible, since, owing to the ease of public access to the bog, artificial marking points could not be left out overnight. The lines actually used were defined by natural landmarks.

### (a) Drainage system

The system of west-running streams which drain the bog are not fully shown on the 6 in. O.S. maps. The present survey made it possible to fill this gap to a great extent, though the method of survey did not allow any great accuracy of mapping. Fig. 1 and other diagrams give the information so obtained.

It is clear that large areas of the bog are not under any immediate influence of open drainage channels, and the way in which the water-table is maintained at the surface over most of the bog at the present time suggests that drainage effects are very localized. It must be mentioned that the artificial drains at the south-east corner are now hardly functional, being choked with vegetation in places, and usually full of water elsewhere. It is very probable that they once played a large part in determining the surface vegetation, but these effects, although in the past, are sufficiently recent to belong to the 'present-day ecology' and are therefore not discussed further.

There is, however, a point of much significance with regard to the natural streams running westwards, namely that over most of their course through the bog, they are cut back through the peat, so as to expose bare peat surfaces on their banks. It is only for short distances upstream from the road bridges that there exists what one may regard as the condition of an original or primary drainage channel—distances of 300 m. up Burbage Brook and 150 m. up East Brook (so named for ease of reference; no name appears on the published maps). By a primary drainage channel is meant a channel which was present at the beginning of peat formation and never submerged by it, showing in consequence a continuous vegetation cover right to the water edge.

This means in fact that nearly all the existing channel system is younger than the main peat mass of the bog. Quite how one should date the onset of this secondary channel formation does not seem certain at present, though we shall have a suggestion to make on this point when other data have been brought forward.

#### (b) *Surface contours*

The surface contours derived from this survey are given in Fig. 1. The published O.S. maps were not helpful in the matter of contour lines, and in fact the Derbyshire half of the 6 in. sheet (on which Fig. 1 is based) lacked them entirely, and the 1300, 1350, 1400, and 1450 ft. contours have had to be taken from the 1 in. O.S. sheet. The remaining contours of Fig. 1 are sketched in by guesswork, to convey some idea of the terrain immediately surrounding the bog.

Fig. 1 indicates the rapid rise of ground-level eastwards from Burbage Brook, and in fact the appearance of the ground here strikingly recalls the 'rand' region of a raised bog. The similarity is heightened by the presence on these slopes of frequent *Molinia* tussocks, a species occurring only in one or two small tufts over the whole of the rest of the bog. Further east, the surface slopes up very gradually to the eastern watershed and, on the north, to the foot of the low ridge which runs westwards from Rud Hill and forms the northern boundary of the bog.

#### (c) *Peat depths and original surface contours*

From the results obtained with regard to peat depths, it is possible by interpolation to make a diagram (Fig. 3) showing lines of equal peat depth. At first sight the diagram suggests either a raised bog with two main centres of growth, or an infilled basin with two deeper hollows. Figs. 4 and 5 give us the data by which we must weigh these interpretations. Fig. 4 is, of course, constructed from peat depths and surface levels at the bore-points, and gives a rough idea of the land surface existing before peat formation started. There is an entire lack of evidence of any original lake basin or basins, and this idea is borne out by the character of the mineral matter brought up by the borer—a point to be

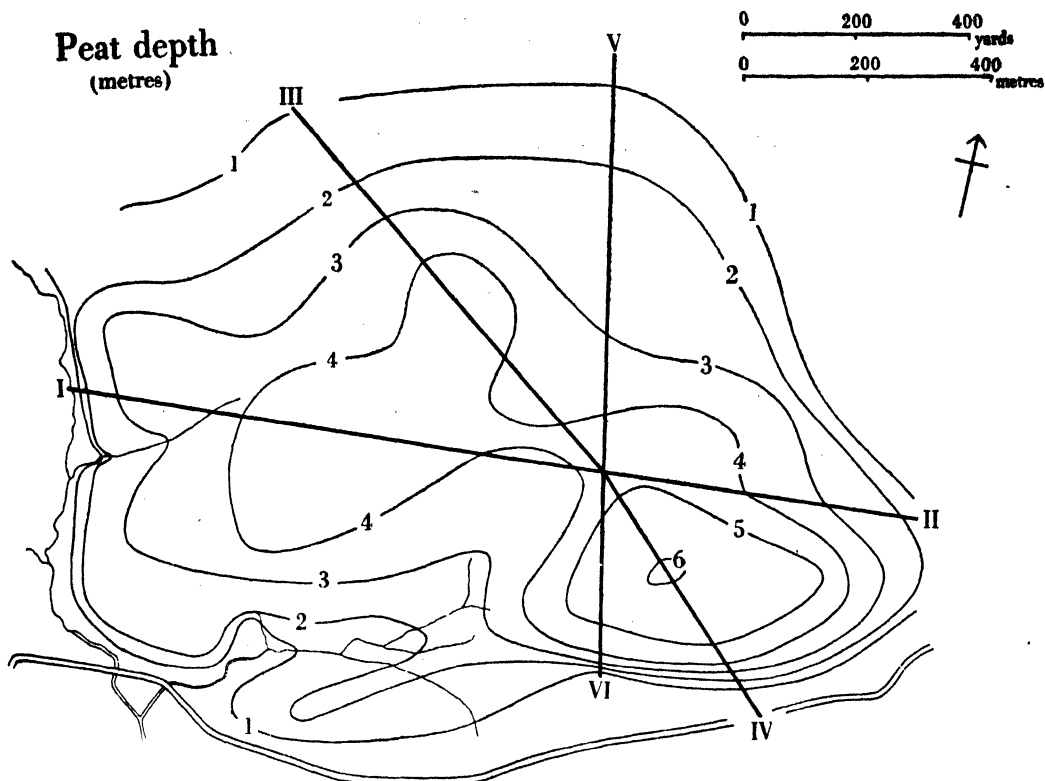


Fig. 3. Distribution of peat depths over the bog surface, given by lines of equal depth. The section lines labelled with roman numerals are shown in profile in Fig. 5.

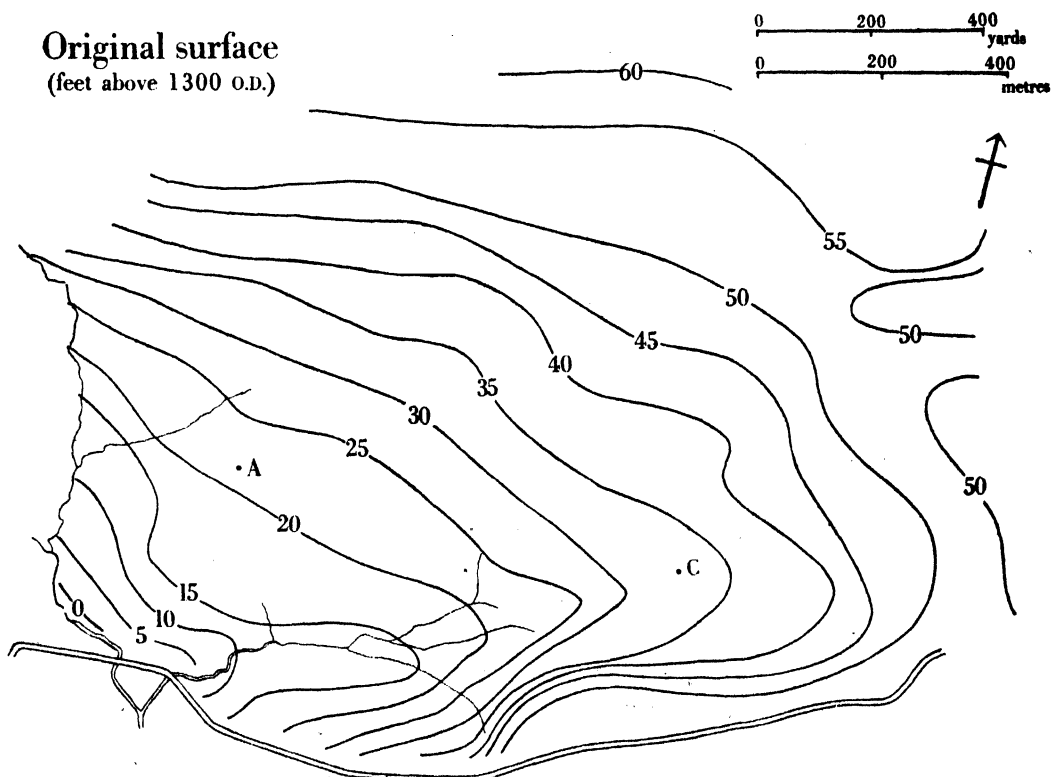


Fig. 4. Contours of the original mineral soil surface before peat formation started.

described shortly. Naturally enough, however, the ground was not a mathematician's plane, though it showed a general south-westwards slope; it was characterized by one well-defined trough in the general direction of the present-day East Brook, and probably another one, much less well-defined, running roughly north-eastwards, and draining into Burbage Brook perhaps where the present smaller eastern tributary joins it. It is clear also that the deepest peat occurs in the regions at the heads of these two troughs in the original surface.

Fig. 3 gives the positions of the section lines which are shown as profiles in Fig. 5. Sections III-IV and V-VI merely exhibit over again what has just been suggested, namely that the growth-rate of the peat has been more rapid, or else started earlier, in the

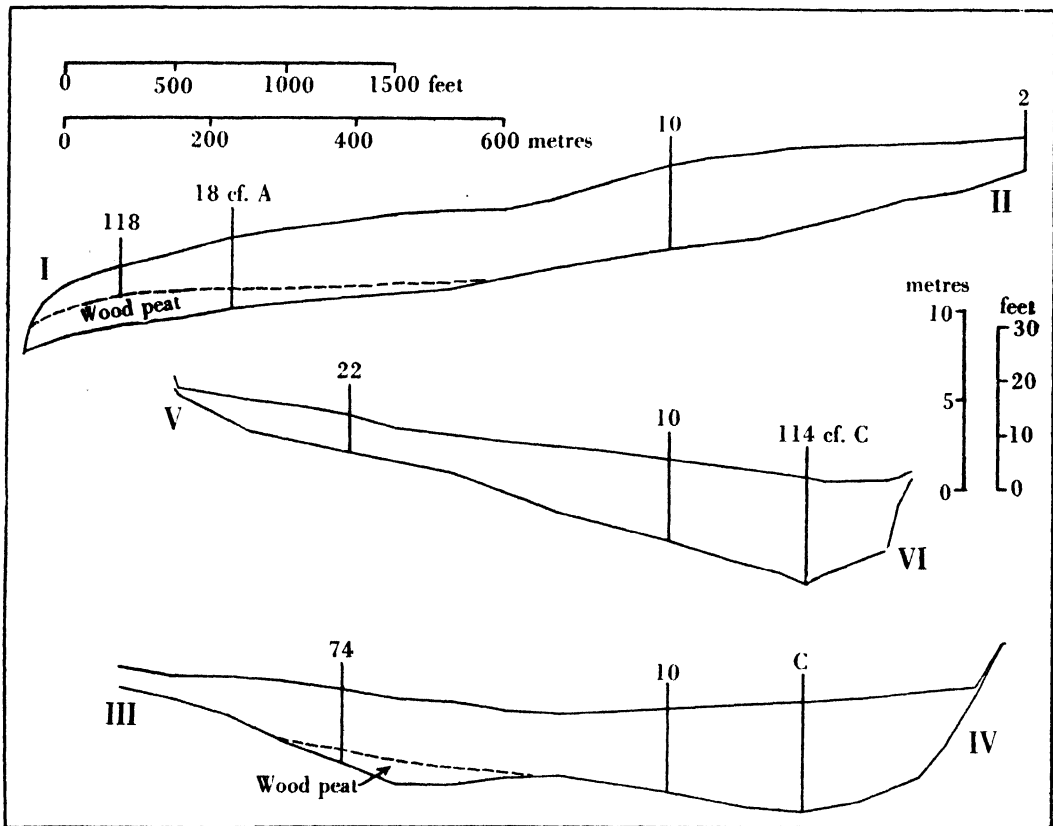


Fig. 5. Sections across the bog along the lines shown in Fig. 3. The numbered sites refer to profiles which are illustrated in other figures, except for sites 18 and 114, which are exactly similar to profiles A and C respectively.

moisture collecting hollows of the ground. Section I-II, on the other hand, does suggest that there is a sense in which the surface of the bog may be said to be convex relative to the underlying ground surface. Again, bog growth at the south-west corner has been limited and retarded by the presence of persistent primary drainage channels, so that on both counts we may see traces of the characteristics of a raised bog.

#### (d) *Bog stratigraphy*

Fig. 2 shows that the profiles examined were widely scattered over the bog, and from them it is possible to draw a general notion of the bog peats. First, however, a word about the mineral substratum. The borer occasionally struck hard rock immediately below the



peat. Sometimes it met coarse sand which was very resistant, but most often it was possible to push the borer down a few decimetres and bring up a sample of the material. This was nearly always a mixture of sand and clay. The latter was occasionally soft and penetrable and bluish in colour, but was never entirely free from grit, and graded imperceptibly into coarser material. Sometimes pieces of readily crumbled sandstone were included, and the general impression, to a non-geologist at any rate, was that of a mineral soil derived by the weathering *in situ* of the characteristic rocks of the neighbourhood—millstone grit and associated shales.

Turning to the nature of the peat, one may broadly say that this is a *Sphagnum* bog, since the great mass of the peat has been produced by a vegetation in which *Sphagnum* was dominant or very abundant. We have already described the fact that in the central parts of the bog, *Sphagnum* peat is found within 5 cm. of the surface, and the profiles of Fig. 6, and those given in Figs. 8 and 9, may be taken as illustrations. The most basal layers of peat, however, were not *Sphagnum* dominated in any part of the bog; that is to say, the basal peat was amorphous in the hand, and in those cases where it was examined microscopically *Sphagnum* leaves were almost entirely absent. This accords with the common observation that bog *Sphagna* do not grow directly on a mineral soil. Passing upwards from these basal peats there is a gradual transition to highly humified *Sphagnum* peat, and then a progressive freshening of the *Sphagnum* towards the upper surface.

Nowhere, however, was anything found which suggested the presence of a well-marked stratigraphical horizon (the 'Grenz' horizon) such as those which have been described from lowland bogs. This may have been due to inexperience in dealing with borer cores from a saturated bog, but support is given to the idea that the absence is genuine, by the closer investigation of the pollen analysis series, and also by widespread observations on exposed profiles in eroded blanket peats in the southern Pennines and elsewhere in the north of Britain. It might therefore be concluded that blanket peats at this altitude are all post-'Grenz' in date. Alternatively it may be that a lowland bog is a more sensitive recorder of the climatic change which was responsible for the formation of the 'Grenz' horizon, and in examining peats at higher altitudes we have to look for the parallel effects in some other or more subtle expression of vegetational response. That this latter interpretation is the correct one is clear from work on southern Pennine peats as a whole and will be demonstrated from Ringinglow bog by the pollen analytical results shortly to be described.

Within this generalized description of the bog peat there is need to distinguish certain differences between one part of the bog and another. Thus the really fresh and well preserved *Sphagnum* layers are confined to the upper 2 m. of peat in the central bog region in the neighbourhood of sites 10 and C. In these layers *Sphagna* of the *cymbifolia* group are conspicuous. Below them, and in other parts of the bog, the *Sphagnum* is not so fresh, and the phrase 'mid-brown slushy *Sphagnum*' is perhaps the one most commonly recurring in the field notes. In the *Juncus* flush region at the north-west corner, no recognizable *Sphagnum* peat was seen in the field. The peat of this area has not been examined in detail, but it is shallow (see Fig. 3) and quite possibly the vegetation in this area has always been of the 'flush' type.

*Calluna* remains are on the whole more prominent in the profiles of the western end of the bog, while *Eriophorum* is a fairly constant component throughout. Sometimes it comes up in tufts in the borer, recognizable as *E. vaginatum*. More often it is represented

by tough roots, many of which have the pinkish colour characteristic of *E. angustifolium*. Both types of root have a binding effect on the *Sphagnum* matrix, so that coherent cylinders 20–30 m. long, can be pulled out of the borer chamber. This 'stringy' character of the peat was of widespread occurrence and not confined to particular horizons, though on the whole it was most marked in the upper 2 m. of the deeper profiles.

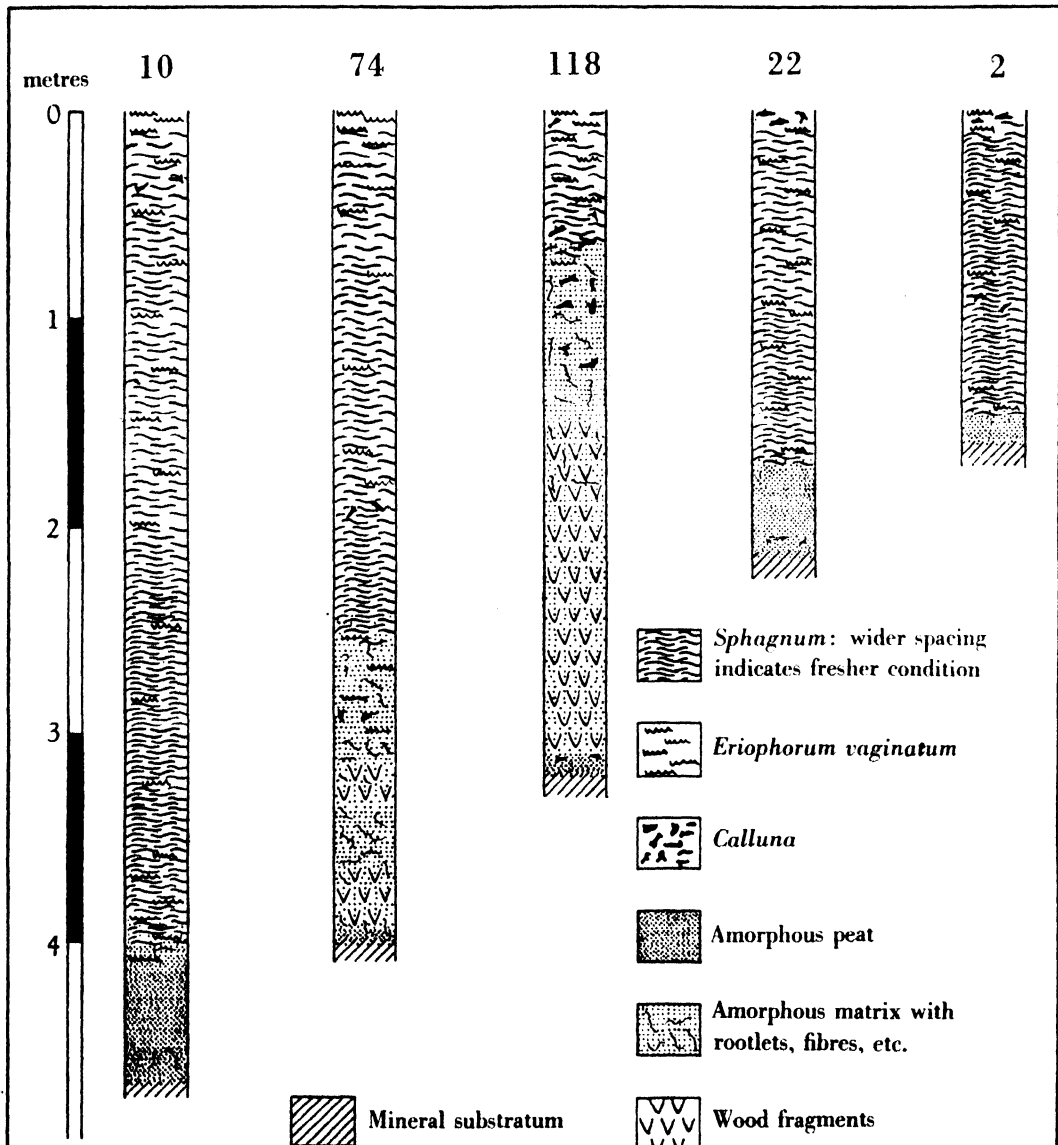


Fig. 6. Profile diagrams made from field notes. The positions of the profile-sites are indicated in Figs. 2 and 5.

It is in the basal peat layers that the strongest regional differentiation is shown. In the shallower peats of the northern and eastern stretches, a shallow layer of amorphous peat passes quickly over to *Sphagnum* peat as illustrated by the profiles of sites 2 and 22, in Fig. 6. Fig. 5 shows how these and the other profiles of Fig. 6 are placed in relation to the bog as a whole. The deeper profiles of sites 10 and C (the latter given in Fig. 8) show greater depths of amorphous peat, while site C shows a long gradual transition region

below the level at which *Sphagnum* is recognizable in the field. It must be emphasized that the profile diagrams are direct symbolizations of the field notes and not results of detailed examination of the peats in the laboratory. It is probable that *Sphagnum* was present in the vegetation forming this transition region, since its leaves were found in the samples from site C at this level, taken for pollen analysis. The only structures visible in the field amongst the amorphous matrix were roots and rootlets, many of them monocotyledonous, and a fair number ericaceous in appearance, together with long fibrous strands probably belonging to monocotyledonous leaves.

Further west than site 10 we begin to reach the profiles where wood peat forms the basal layers. Sometimes, as at site 118 (Fig. 6), there is a considerable depth of wood peat with not a great deal of bog peat above it. This type of profile was only found close to Burbage Brook and, as the section I-II in Fig. 5 indicates, the wood peat thins out in passing eastwards from the brook. Fig. 7 gives a fair idea of the area of distribution of the basal wood peat; it covers the evidence not only of the investigated profiles, but of the depth probings also, from which the basal peat samples were brought up and examined. The diagram shows that in the western parts of the bog, wood fragments were found wherever the borer was put in, suggesting a close and long-lasting woodland cover. Further east, there was not this constant occurrence of wood remains, but there are scattered records, and one should not hastily conclude that half the bog was wooded and half was bare. Rather one may visualize a dense woodland occupying the better-drained region around the headwaters of Burbage Brook while, further afield, a more open damp-heath-woodland type occupied the regions with less effective drainage, in which bog conditions more quickly established themselves at the expense of trees and scrub.

Fig. 7 shows the results of a few depth probes which lay outside the area of the main survey, and whose position on the map is therefore only approximate. Peat depths and presence or absence of basal wood peat is indicated. The long series, stretching across the western bog, is of some interest, showing that considerable peat depths extend almost out to the escarpment, and suggesting that this area has had a comparable history to that of Ringinglow bog. The records of wood peat in the western bog are also worth noting since, though few in number, they suggest that the woodland extended some way from the main drainage channels, and it is therefore possible that shelter from the full force of westerly gales may have been one factor in determining the distribution of the woodland. However that may be, the evidence of Figs. 5 and 7 shows a fairly clear relation between amount of wood peat and ease of drainage, and this must have been the major determining factor.

Most of the wood fragments which were examined were found to be of the alder-birch type, and birch bark was always catching the eye during the field investigations. The fragments which were brought up in the borer were not usually in good condition for recognition. Much better specimens were obtainable from the exposed peat faces in the banks of Burbage Brook and East Brook. The results of laboratory investigation of the wood types are as follows:

Out of twelve better specimens from the stream banks: five alder, four probably alder; two birch, one probably birch.

Out of seventeen poor specimens taken out of the borer: one alder, three probably alder; one birch, one probably birch; nine alder-birch type, too poor for closer identification; two others, not identified, possibly *Salix*.

Clearly alder and birch are the main trees, with alder probably predominant.

# Distribution of wood peat

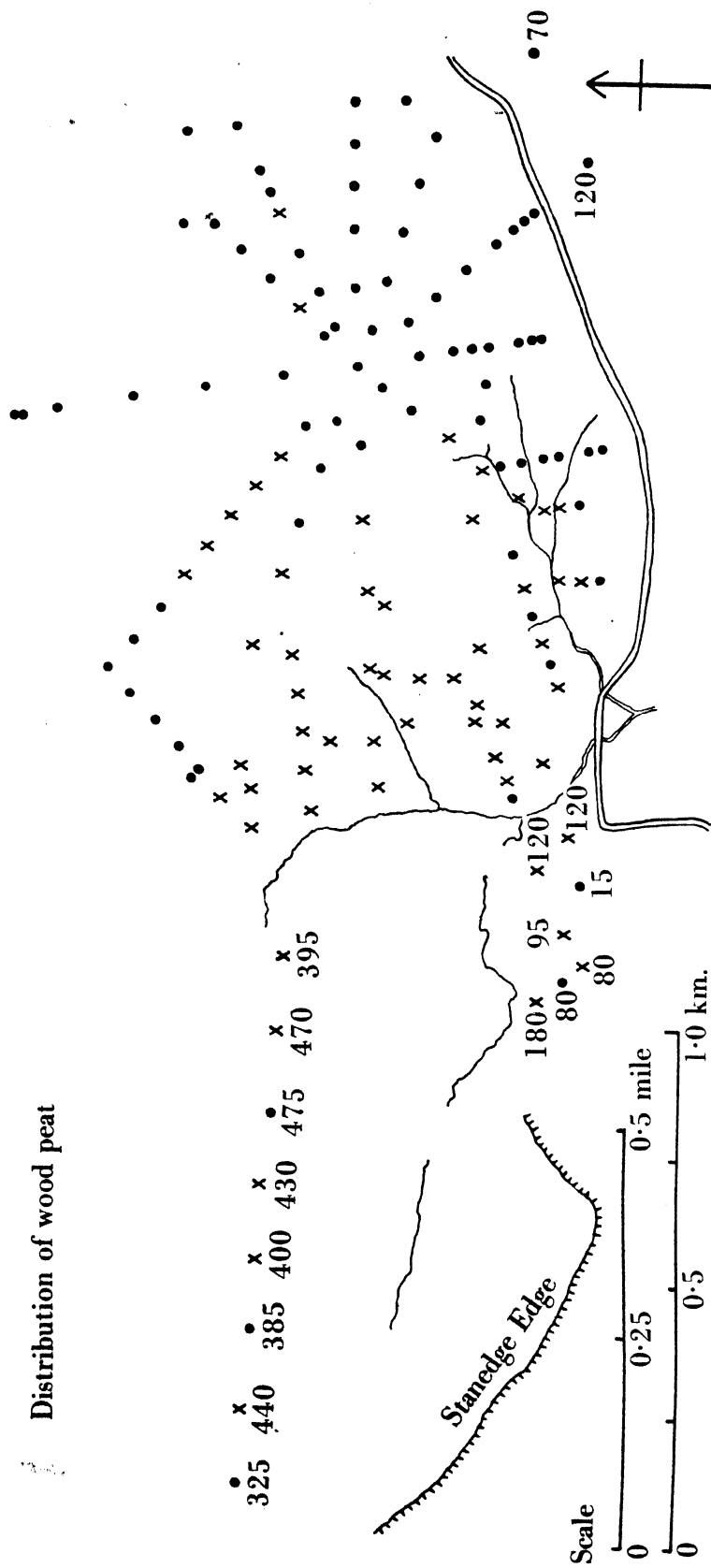


Fig. 7. x Sites where wood fragments were brought up by the borer. • Sites where no wood was found. The depth of peat in cm. is indicated for a number of sites not covered by Fig. 3.

## 3. INVESTIGATIONS BY POLLEN ANALYSIS

On the basis of the general bog structure, two sites were chosen for taking samples for pollen analysis. One, site C, was taken at the place where the greatest depth of peat was recorded, with the hope of getting a diagram starting as early as possible. The other, site A, was taken in a region with a thick basal layer of wood peat, but not under the close influence of any drainage channel which is likely to have existed previously, judging from the contours of the original mineral surface (Fig. 4).

Samples were collected at intervals of 5 cm. over most of the depth, but closer together at the base. As the diagrams show, however, the samples actually analysed were spaced much further apart. The upper 50 cm. of peat at site C was very troublesome since the borer did not deal satisfactorily with the almost unhumified tough mass of *Sphagnum* and *Eriophorum* roots. In the end a column about 50 cm. deep was dug out from a spot close to the boring, and samples taken from measured positions down the column.

Pollen preparations were made by macerating in 10% KOH, and mounting in glycerin jelly containing safranin. Certain details of the procedure will be dealt with in another context. The coarser debris was filtered off and examined separately. 150 tree pollen grains were counted for each sample. This 150 included *Pinus*, *Betula*, *Quercus*, *Ulmus*, *Tilia*, *Alnus* and *Fagus*, the 'standard list' of trees for British diagrams. *Fraxinus* was counted, but not included in the 150 grains. This procedure has no ecological justification, but was necessary because *Fraxinus* has not been included in the majority of British diagrams published up to date, and hence if it were included in the Ringinglow 'tree' count, the percentages for trees in the 'standard list' would not be comparable with those in diagrams from other British localities.

*Site C**(a) Tree-pollen curves*

The tree-pollen frequencies are shown on the left-hand side of Fig. 8. A great many points of interest arise out of these curves, but it must be stated clearly that no attempt is made in this paper to discuss the results in relation to the general forest history of the region, except in the broadest way, and except where it is relevant to the history of bog development with which we are concerned. The tree-pollen curves form, as it were, a framework to which we may attach our conclusions as to the phases of the local ecology, since it is the tree data alone which can form a link with the general sequence of events in post-glacial times, the sequence which is now expressed in Godwin's 'zonation' scheme for England and Wales. Considering first then the zoning of the diagram, it is clear from the behaviour of the *Betula*, *Tilia* and *Fagus* curves that the diagram covers some of zone VII and, therefore, all of zone VIII. Further, the *Pinus-Alnus* relationship at the base of the diagram shows that the beginning of zone VII is included. Since this point may be obscured by the necessarily compressed scale of the diagram, the numerical values are here given for the basal seven samples:

Sample depth (cm.)	<i>Pinus</i> (%)	<i>Alnus</i> (%)
585	7	43
590	17	25
595	19	24
600	23	29
605	21	25
607.5	30	19
609	34	13

That is to say, peat formation started at this site at the time of the Boreal-Atlantic transition. Godwin's subdivision of VII into VIIa and VIIb is also indicated by earlier higher values of *Ulmus* and there is a very striking behaviour of *Corylus* at about the level where *Ulmus* is changing. A number of other southern Pennine pollen diagrams, not yet published, show that this feature of the *Corylus* curves is constantly associated with the VIIa-VIIb transition, and I have therefore used *Corylus* rather than *Ulmus* to fix the position of the dividing line, since the *Ulmus* change is ill-defined. The line is drawn at the start of the *Corylus* rise, on the assumption that the latter is a response to a preceding change in conditions.

The phase of the diagrams which is here called 'Transition' covers the period of change in the tree-pollen curves from the typical VIIb spectrum to the typical VIII spectrum, and the upper limit is drawn at that level at which the change appears to be complete. The lower limit, at 410 cm., is not, however, based on the tree-pollen curves, but taken at the level of the '*Menyanthes* horizon' obtained from the right-hand half of the diagram. This point will be discussed later.

Finally, the upper part of the diagram has been de-limited as a definite phase, referred to as 'VIII mod.', beginning at the depth of 100 cm. and lasting to the present bog surface. At the beginning of VIII mod. there are changes in the whole pollen picture which appear to be completely explicable in terms of the direct or indirect action of the human population on the regional vegetation. In other words, it is at this stage that forest destruction set in on the grand scale in those areas of forest whose pollen had previously formed the major component of the tree-pollen rain on the bog surface.

The starting point of VIII mod. is actually based on the non-tree pollen curves, but the tree-pollen curves themselves show changed proportions. *Betula*, *Alnus* and *Corylus* fall steadily, while *Fraxinus* rises; later there is an obvious influence of plantations of *Pinus* and *Fagus*, and at the very end there appear the effects of selective preservation of *Ulmus*, the present-day hedgerow tree of northern England. The designation VIII mod. has been preferred rather than IX, since there is no evidence for any large-scale climatic cause for the pollen changes, such as may generally be held responsible for the differentiation of one zone from another in the post-glacial scheme as a whole.

Much more will be written about these tree-pollen curves in a future publication when it will be possible to deal with them fully in relation to other southern Pennine pollen diagrams, and to British forest history as a whole. Here we must now turn to the remaining data of Fig. 8, which lead us to the heart of the present subject.

#### (b) *Stratigraphy, non-tree pollen, etc.*

*Tree-pollen frequency and non-tree/tree ratio.* The relative tree-pollen frequencies for each sample were obtained by using quantitative methods of preparing the slides. A known weight of the still moist peat was taken from the sample tubes for maceration; 0.5 g. from samples likely to be rich in pollen, 1.0 g. for poorer samples. Since the undried peat has a very high moisture content, this method amounts in effect to using equal volumes of peat. The pollen residue from the centrifuge was mixed with a standard volume of glycerine jelly, and from the well stirred mixture a standard volume was spread on to a slide and covered with a cover-glass always of the same area. Three such standard slides were made from each sample, and all used in the counting. Then a note was made of the number of traverses of a slide which were needed to obtain the count of 150 tree

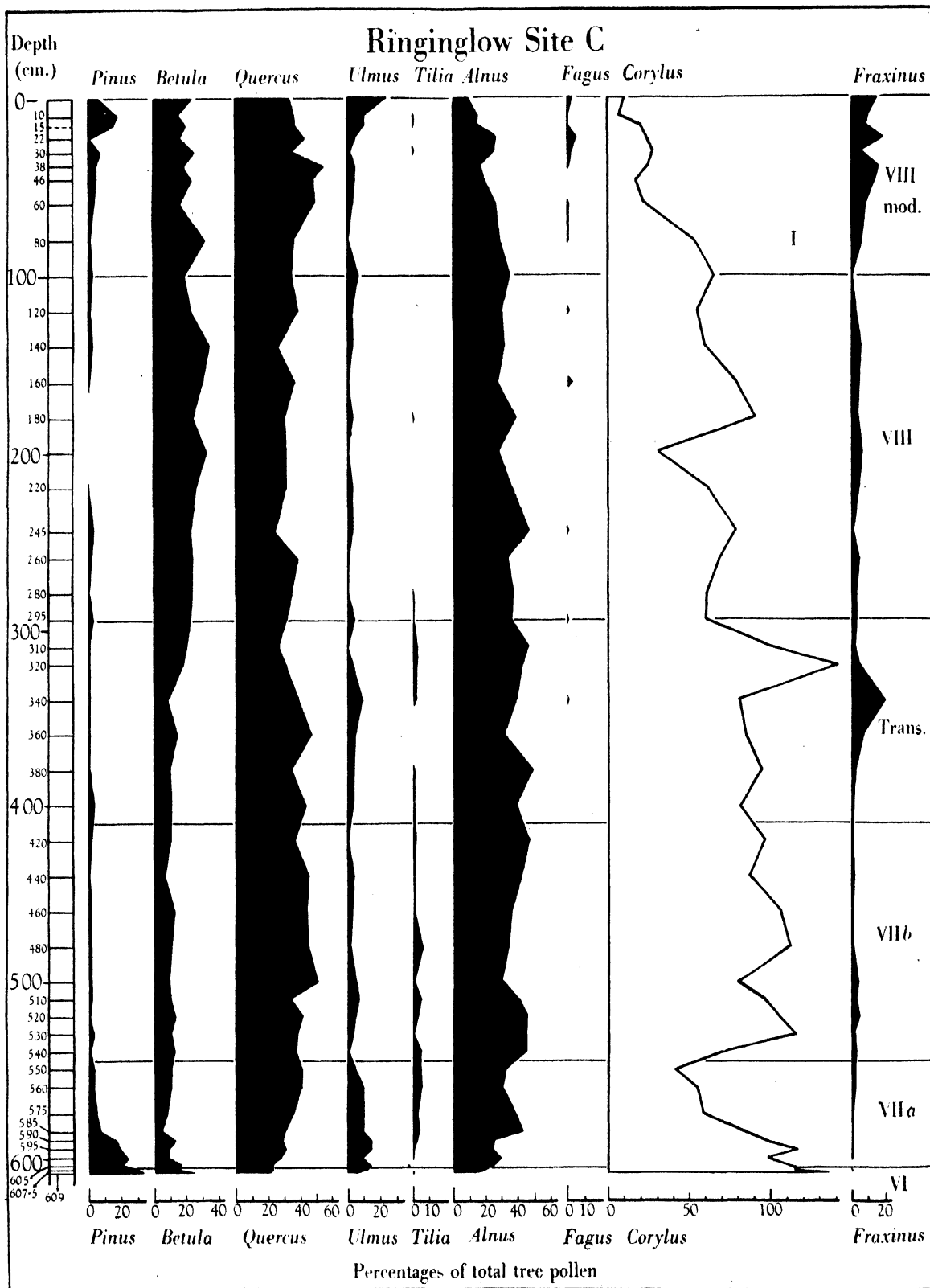


Fig. 8.

Figs. 8 and 9. Pollen diagrams for sites C and A. ○ *Menyanthes* seeds. *M.*, *Menyanthes* pollen. ● *Sphagnum imbricatum*.  
 - *Juncus* seeds. *P.*, *Potentilla* pollen. *I.*, *Ilex* pollen. *D.*, *Drosera* pollen. Stratigraphic symbols as in Fig. 6.

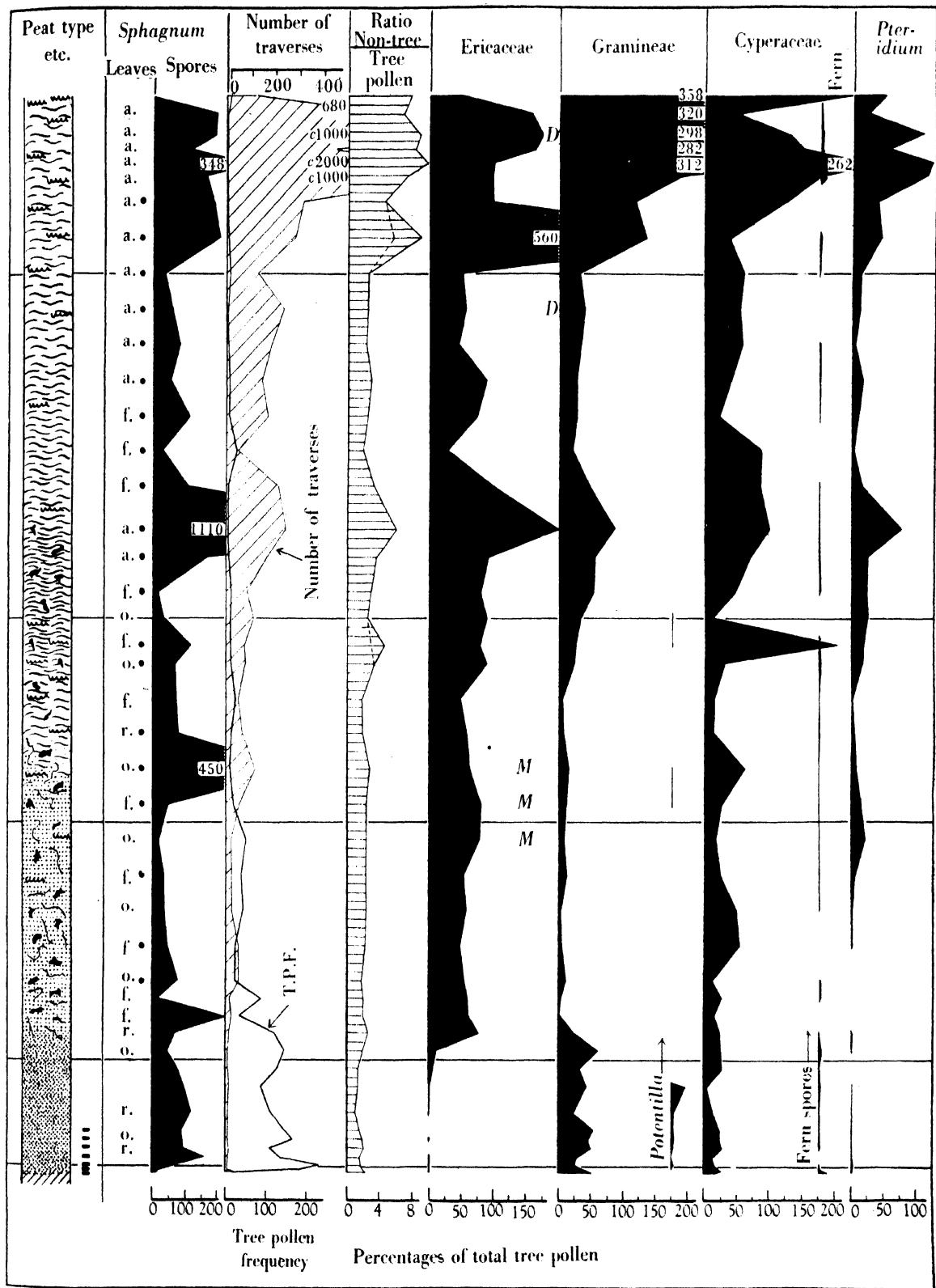


Fig. 8.



pollens. The figures plotted in Fig. 8 under the heading 'Number of traverses' are actually the number of traverses for 150 tree pollens for 0.5 g. fresh peat. Then the relative tree-pollen frequency (T.P.F.) is taken as  $1000/\text{number of traverses}$ . Since the T.P.F. is very low in the upper part of the diagram, the number of traverses has also been plotted, so that the variations may be visible.

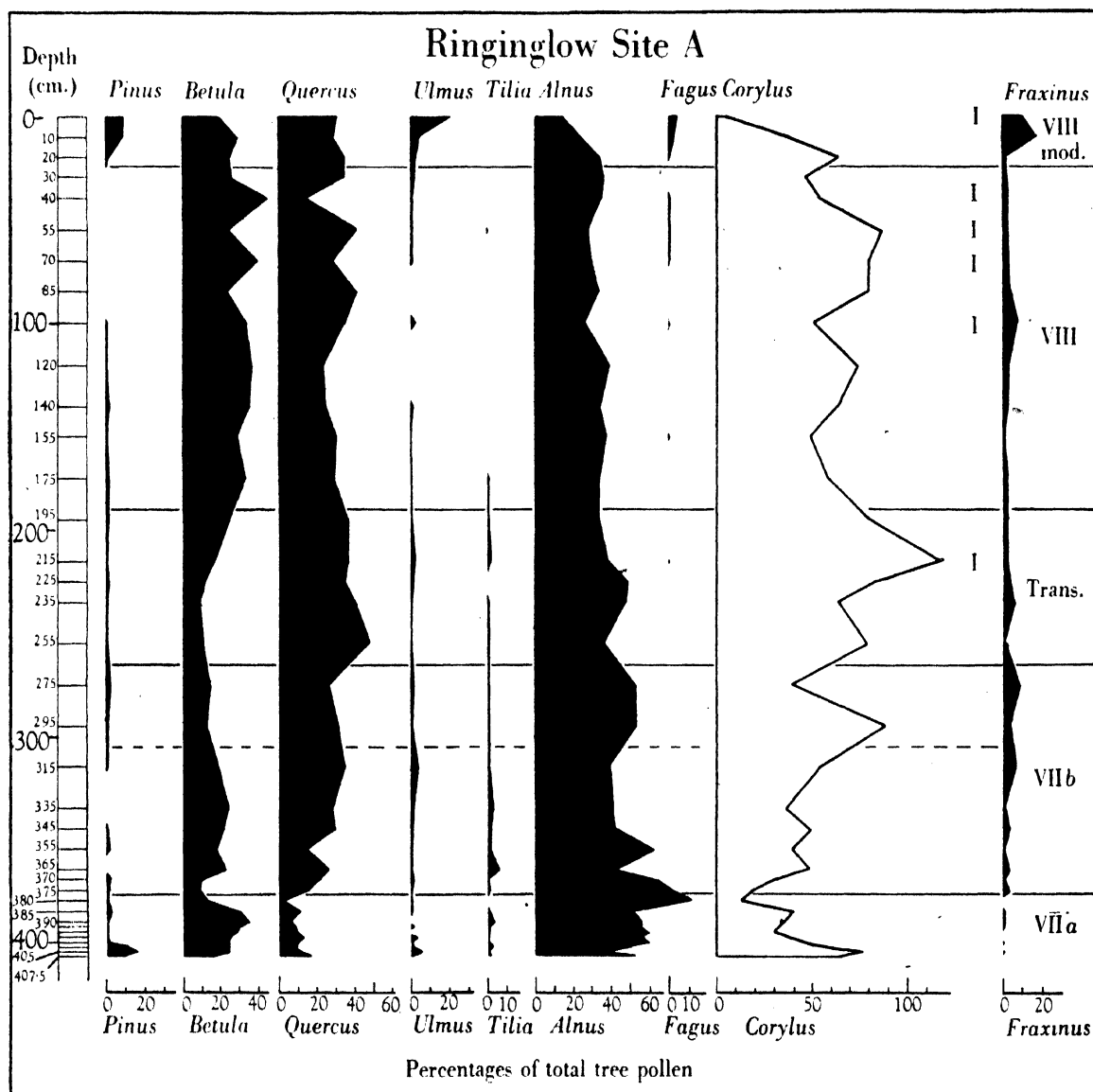


Fig. 9.

Now if the total annual tree-pollen rain remains constant, then the tree-pollen content per unit volume of peat will be inversely proportional to the rate of peat accumulation; in other words, the curve for number of traverses will express the rate of upgrowth of the bog surface at any period. How though can one judge whether the annual tree-pollen rain is constant or not? The answer lies in the curve for Non-tree/Tree pollen ratio (NT/T). The non-tree pollen is assumed to consist mainly of the immediately local, or 'bog' component

and therefore to contribute a roughly constant quota to the total annual pollen rain.\* Hence a big change in NT/T should be a reflexion of a change in the tree-pollen rain. Conversely, if we find a large change in the T.P.F., without any corresponding change in NT/T we shall assume that the phenomenon involved is one of changing rate of bog growth and not of changed regional forest cover.

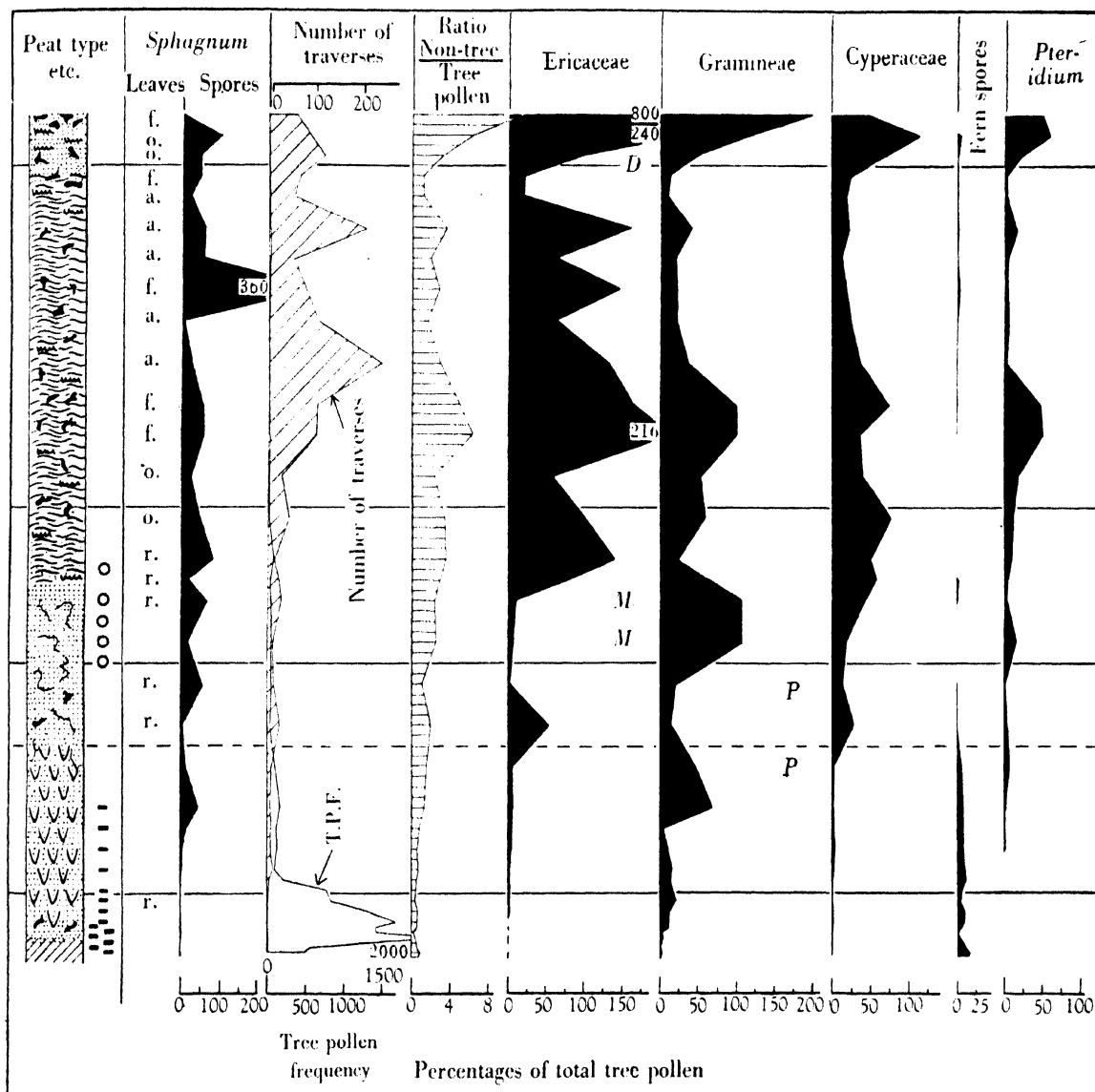


Fig. 9.

The data plotted in Fig. 8 show that while there are vast changes in the values for T.P.F., the values for NT/T show a surprising constancy, by comparison, until the beginning of VIII mod. Thus while NT/T values range from 1 to 5, with a pretty steady

\* In actual fact the figure for NT pollen for each sample is obtained by summing all the pollen other than the standard list of trees, except that Bryophyte spores are omitted as they show such wild fluctuations. However, what might be regarded as 'non-local' pollen forms only a very small fraction of the total, until the beginning of VIII mod.

average about 2, the T.P.F. figures show maximum values 50 times as great as the minimum values. Therefore it seems not unreasonable to adopt the suggestion just put forward, namely that the curve for number of traverses expresses, broadly speaking, the rate of growth of the bog.

At the base, the high T.P.F. values express the slow rate of peat accumulation which is manifested also by the highly humified amorphous nature of the peat. A small allowance must be made, however, for slightly lower NT/T values between 550 and 570 cm., which is no doubt a reflexion of the local woodland cover at the west end of the bog. Then, early in VIIb, comes a huge fall in T.P.F. with no effects visible at all in the NT/T curve, and every available line of evidence suggests this as a major switch-over in the type of bog cover and rate of peat accumulation. The beginning of this change coincides with the *Ulmus* horizon, and there may well be a causal connexion. On the other hand, even under a constant climate one would expect this kind of change from the pioneer bog-initiating species to the characteristic and faster growing bog dominants, especially *Sphagnum* spp. For the time being we shall adopt the simpler view of this change as being merely 'successional'.

Then between 420 and 400 cm. there is a fairly sudden change in T.P.F. which shows a threefold increase in rate of bog growth, again without marked alteration of NT/T. Now at about this level there occurs the lower of the only three records of *Menyanthes* pollen at this site. At site A (Fig. 9), at a precisely corresponding level, *Menyanthes* pollen again begins to occur, and not only that, but *Menyanthes* seeds are found in quantity. It is impossible to regard this as an insignificant coincidence; rather it must mean a considerable abundance of the plant over the bog surface, appearing rather suddenly but persisting for some time. Considering the ecological characteristics of *Menyanthes*, together with the sudden increase in growth-rate of a bog surface which was presumably already mature, it is surely clear that we are dealing here with a sudden increase in wetness in the environmental conditions. At this altitude, only a change in climate could account for this, and the obvious inference is that we have here the equivalent of one of Granlund's 'recurrence horizons' (RY). Since the evidence indicates that this level represents the most drastic change in bog conditions between the *Ulmus* horizon and the present surface, one might have been inclined to take it as homologous with Granlund's RY III, which has hitherto been accepted as the main stratigraphical 'Grenz' in all ombrogenous bogs. Indeed, I had accepted this interpretation myself until the conclusions recently expressed by Godwin\* put the matter in a new light. He has clarified the position concerning the VII-VIII transition zone in his scheme by postulating not only that while RY III (dated roughly at 500 B.C.) lies at the end of the period, the preceding recurrence horizon (RY IV, dated roughly at 1200 B.C.) forms the starting-point of the period, but also that RY IV may in some places show an increase in wetness whose effect may be as great as, or in some cases greater than, that associated with RY III.

This brings harmony into a number of discrepancies which have hitherto arisen in any attempt to correlate the stratigraphy and dating of a wide range of English and Irish bog types. The Ringinglow data will also fit well into Godwin's scheme if the main 'Grenz' level is taken to lie at the top of Transition, i.e. at about 290 cm., while the '*Menyanthes* horizon' at 410 cm. represents the preceding recurrence horizon (RY IV of Granlund), and this is therefore the interpretation here accepted. Examination of Fig. 8 shows a marked drop

\* Lecture to the Prehistorical Society, 12 June 1946.

in general level of tree-pollen frequency (i.e. rise in number of traverses) just above the top of Transition and this is the clearest indication given by the data of the existence of a 'Grenz' at this level.

Just below this, at 310 cm., there is a sudden peak in the NT/T curve which is caused entirely by the sudden maximum in the Cyperaceous curve. The dotted line shows how the NT/T curve would run if the Cyperaceous peak were removed. These occasional violences are almost inevitable with the 'local' components of the pollen rain and cannot be taken to be of general significance when they are confined to a single sample. A similar case is seen again at 80 cm., where this time Ericaceous pollen is to blame, and here again the 'smoothed' value of the NT/T curve is indicated.

At 245 cm., however, there is a peak value in NT/T, and corresponding peaks in all the main NT curves. Moreover, all the NT/T values in this early part of VIII are above the average for the whole profile, and at the same time the number of traverses shows much enhanced values. The increased NT/T values would not by any means entirely account for the whole rise in number of traverses, but must contribute something to it. Put more directly, there must at this time be a genuine slight lowering in the average tree-pollen rain. This brings out an important precaution which has to be observed when the NT curves are being used to interpret the nature of the bog surface at different stages. The NT figures are given as percentages of the total tree pollen. Hence, if at any time the tree pollen is scarcer for any reason, the NT pollen figures will automatically be increased, although there is no real increase in the absolute pollen rain of the NT species on to the bog surface. To return to the part of the diagram we are considering, this means that the maxima in *Sphagnum*, Ericaceae, Gramineae, Cyperaceae and *Pteridium*, which are seen at 245 cm. are all false maxima, that is to say they do not represent a sudden increase in the abundance of these species on the living surface of the bog at that date. Similarly we may regard the values in all these curves during the first part of VIII as being over-emphasized from the point of view of the bog ecology, and the phenomenon will be referred to in subsequent pages as 'over-emphasis'.

At 200 cm. may be seen the exactly converse phenomenon, a temporary rise in the T.P.F. correlated with false minima in the main NT curves. Since this affects only one sample it is probably best to regard it provisionally as accidental in nature.

Apart from these rather doubtful questions concerning the tree-pollen rain, there is a greater average growth-rate of peat in zone VIII than in the Transition zone and on the whole a gradually increasing rate, parallel with the increasing freshness of the *Sphagnum* peat. When we come to VIII mod., however, both T.P.F. and NT/T show enormous changes, without any change in the nature of the peat. Here, then, it is genuinely the tree-pollen rain which has been affected. If it is correct to interpret this in terms of widespread forest destruction, and it is hard to do otherwise, then not only do all the 'local' pollen components show 'over-emphasis' throughout VIII mod., but non-tree pollen must be playing a large part in the 'regional' component of the pollen rain.

There seems to be a definite though slight recovery in the very uppermost part of the NT/T curve, which reaches its absolute maximum at 38 cm. This may well be an expression of the attempts made by landowners during the last three centuries or so to compensate to a small extent for the loss of the natural forests by making plantations. The idea is supported by the pollen curves for pine and beech, both of which increase notably in these youngest horizons and which are known to have been extensively planted.

The surface sample, scraped from the actual peat surface, shows the same high NT/T value as those samples in the upper peat layers but, strikingly enough, a much higher T.P.F., indicating the sudden slowing of bog growth during the short span of years which has passed since the *Sphagnum* surface was replaced by the much more slowly growing cotton grass community.

*Sphagna*. Spores occur throughout the profile, and the curve shows occasional sudden peaks which might well be taken as causally related to the climatic changes associated with 'Grenz' phenomena. This correlation could however be fortuitous, since *Sphagnum* spore curves in southern Pennine diagrams often show wild fluctuations. The values in VIIa are surprisingly high considering the virtual absence of leaves; possibly the prevailing conditions favoured heavy fruiting of scattered patches of *Sphagnum*, or else favoured species which are normally abundant fruiters. Spore values are consistently low in VIIb—lower, in fact, than in any other zone. The very high values of VIII mod. are, of course, all due to over-emphasis.

The records of *Sphagnum* leaves were made on the residues from the pollen preparations. The frequency symbols are very inadequate, but they serve at least to convey the notion of gradually increasing *Sphagnum* dominance from the base of the bog to the top. The data concerning *S. imbricatum* are noteworthy. It is found both in VII and VIII, though more prominently in the latter, but breaks off sharply at 50 cm. from the surface, being absent at levels higher than this. The middle stretches of the profile (roughly between 350 and 150 cm.) show abundance of a small-leaved *S. acutifolium* type, probably close to *S. acutifolium* Ehrh. itself, though the fossil material is hard to deal with. This species is an important component of all the southern Pennine blanket peat so far examined. At higher levels in this profile it is less important and the main associate of *S. imbricatum* is another Cymbifolium *Sphagnum*, probably *S. medium*. *S. papillosum* was markedly absent throughout most of the profile, though one should perhaps raise the possibility that the characteristic papillae may easily weather away, thus leaving the fossil specimens undistinguished from related species. However that may be, *S. papillosum* did certainly occur in the top 50 cm. of the profile, and may be found with fair frequency in samples of sub-surface peat taken from this area of the bog surface.

*Gramineae*. The eye is at once struck by the marked dominance of grass pollen in the early bog stages. The presence of abundant *Juncus* seeds at the base, the curve for *Potentilla* pollen (probably *P. erecta*), the small quantities of Cyperaceae and the absence of Ericaceae, all suggest a slow growing flush peat with grasses (possibly *Molinia*?) becoming dominant in succession to rushes. It will be remembered that site C lies in what was a trough in the original surface, so that a flush vegetation would naturally develop early there, and persist for a long period, under a generally 'bog-forming' climate.

Grass pollen falls away sharply as the bog-type changes and Ericaceae become important, but it increases again in VIII as compared with VII even when all allowance is made for over-emphasis. In VIII mod. we are dealing not merely with over-emphasis of local grass pollen but far more, as the quite enormous values must indicate, with the replacement of forest by grazing land over vast areas in the northern uplands.

*Cyperaceae*. This curve is generally similar to that for Gramineae except that it shows an increase above the change at 540 cm. or so, instead of a decrease. The abundance of macroscopic *Eriophorum* remains above 450 cm. suggests that this genus accounts for the greater part of the Cyperaceous pollen above this level.

*Ericaceae*. This family enters very abruptly into the bog scenery, but then remains as a continuously important component. When allowance is made, however, for over-emphasis, it appears that the abundance is less in VIII than in VII, in contrast to the situation with *Cyperaceae* and *Gramineae*. This conclusion is borne out by the corresponding lesser frequency of macroscopic remains. The pollen tetrads were almost all of the *Calluna* type; no other type occurred in significant quantities.

To summarize briefly the ecology recorded in this profile; the onset of 'atlantic' climatic conditions allowed the formation of a damp grassy flush in hollow ground surrounded by a rapidly disappearing 'Boreal' forest. Flush vegetation remained until, as we are provisionally assuming, the natural successional changes, probably involving increased soil acidities, allowed the development of bog vegetation, with *Calluna*, *Sphagnum* and *Cyperaceae* as the main components. This bog was slow growing by comparison with more recent *Sphagnum*-bog types; it is perhaps idle to speculate where one might find the present-day representative of such a community until we have a clearer idea of the climatic conditions prevailing in 'atlantic' times.

At the *Menyanthes* horizon bog growth quickened and gradually *Sphagnum* became dominant; a further increase in rate of growth followed at the top of the Transition zone and was associated with increasing freshness of *Sphagnum*, increased importance of grasses and sedges, and slight diminution in that of *Calluna*. There is not enough evidence to decide whether or not the bog surface would have shown a regeneration complex type of structure. In this upper half of the profile one may perhaps suggest that the bog surface was comparable with that now found for instance in the undegenerated regions of Stainmore Forest. At any rate, this rapidly growing *Sphagnum* dominated bog continued unchanged in type right up to a period not more than 150 years ago at the most, and this is a feature of the greatest importance, for it has allowed the making of a pollen record of vegetational changes which are too remote to appear in modern statistical records, yet too recent for recognition in the majority of British peat investigations.

*Pteridium* and fern spores. Though presumably not belonging to the local bog species, these curves merit a brief comment. The fern spores are all of the *Polypodium vulgare* type when the exine is present. They are, however, negligible in numbers except for a marked abundance in the basal layers—part of the ground flora perhaps of the dying Boreal forest. *Pteridium*, on the other hand, is very scanty at the base and first increases appreciably round about the *Menyanthes* horizon. It shows higher values throughout VIII as compared to VII. It is tempting to read here a change in the nature of the forest cover. First, in VII, a tall dense oak forest with associated elm and lime—both casting heavy shade—and possibly a hazel shrub layer as well, with a resultant light intensity too low for bracken; then, in VIII, after a drastic change in climate, a light oak-birch woodland of the well-known *Quercus sessiliflora* type of northern hillsides, on leached soils, with a high internal light intensity and good development of bracken. Finally, the forest clearance of VIII mod. has encouraged the spread of bracken over many parts of the derelict hillsides, and its spores appear in quite large numbers in the pollen samples.

#### Site A

##### (a) Tree-pollen curves.

Fig. 9 gives the data for site A. The stratigraphical column indicates the extent of the basal wood peat, and the dotted line across the diagram indicates the ending of the

woodland cover at this spot. Comparison of Figs. 8 and 9 will show that above this level the tree-pollen curves are very similar and that, below it, the differences may be explained by the effects of the local woodland. The diagram has been zoned by exactly the same methods that were used for Fig. 8. The basal samples show high *Pinus* values and relatively high *Corylus* values, quickly falling, and mean that peat formation at this site also began at the beginning of VII, though with just a little delay compared with site C, so that the *Pinus-Alnus* intersection is just missed, and *Alnus* values start high. This slight difference is easy to understand when it is remembered that site C was in a hollow, while site A was placed on the main convexity of the ground, as shown by Fig. 4.

We have already concluded from the data on the wood structure that alder was the most abundant tree of the local woodland, with birch very frequent, and this is fully confirmed by the pollen data. The high values for these two trees have caused the suppression of the 'regional' tree values, that is, of *Quercus*, *Ulmus*, *Pinus* and *Tilia*, as will be clear if the VIIa sections of Figs. 8 and 9 are compared. This suppression has applied also to *Corylus*, presumably a regional and not a local component, and if the *Corylus* values within the local woodland phase of the diagram were all to be multiplied say by two, to compensate for the suppression, we should obtain a *Corylus* curve for the whole diagram which would agree exactly in general shape with that of site C. One has, of course, to overlook the gross fluctuations which seem inevitably associated with *Corylus* curves, but in southern Pennine diagrams as a whole these fluctuations are not sufficient to obscure an underlying unity of behaviour, a behaviour which is most clearly demonstrated at site C. On these grounds, the *Corylus* rise at site A, between 380 and 365 cm., has again been taken as the ground for dividing VIIb from VIIa. It will be seen that the line drawn purely on this basis coincides remarkably with the beginning of a number of other changes, namely, increase in *Quercus* percentages, fall in *Alnus* to nearly normal values (taking site C as 'normal'), and a very sharp fall in T.P.F. This latter may be taken as before to imply a much increased rate of peat accumulation but, whereas with site C it was possible to explain this without invoking the idea of climatic change, at site A the situation appears more complex, and it is less easy to offer a narrowly 'successional' interpretation. However, the data do not justify further speculation on this point at the moment.

(b) *Stratigraphy, non-tree pollen, etc.*

Taking the stratigraphical column first, it may be seen that apart from the outstanding difference of the wood-peat layer, site A differs from site C in showing a greater prominence of *Calluna* remains, with a corresponding diminution in *Sphagnum* dominance. This is confirmed by the general differences in average levels of the spore curves at the two sites. Again, *Sphagnum imbricatum* was not found in a single sample at site A! This species is obviously exacting, and an understanding of its autecology would be of the greatest value in dealing with peat history.

*Tree-pollen frequency.* It must be noted that the horizontal scales on which T.P.F. and number of traverses are plotted, are different in Figs. 8 and 9. All other scales are the same for the two diagrams.

The T.P.F. values at the base of site A are, of course, of a quite different order from those at site C, owing to the local tree component. During Transition, the values at the two sites are more nearly comparable. During VIII, the site A values are only slightly higher on the whole, indicating a rather slower bog growth-rate here, and this is confirmed by

the fact that while at site C, zone VIII occupies a depth of 195 cm., at site A it occupies 170 cm.

A most striking contrast, however, again reappears in VIII mod. in that, in spite of the great rise in NT/T, the T.P.F. remains relatively high, so that bog growth at site A must have been greatly retarded during this phase. This would explain why VIII mod. occupies such a very shallow depth in comparison with site C, and justifies the conclusion that the same time period is involved at both sites. Confirmation comes also from the highly humified peat at this level in site A, the paucity of *Sphagnum* leaves and the low values of *Sphagnum* spores, when allowance is made for over-emphasis. When we seek for a cause of the difference, the suggestion springs to mind that it was at the beginning of VIII mod. that the western primary drainage channels started to cut their way back through the bog peat, and so established a suddenly improved drainage throughout the south-western section of the bog. No proof of this suggestion lies to hand at present, but no other seems nearly as plausible.

*NT/T ratio and later parts of the non-tree pollen curves.* Little need be said of the NT/T curve except that it reflects the local woodland at the base, and then follows the same broad lines as at site C.

Above the *Menyanthes* horizon, the *Calluna* pollen values are markedly higher than at site C, suggesting that the gradient from better to worse drainage, in passing from west to east along the bog, has been a permanent feature of the bog ecology, with consequently a corresponding slight gradient in growth-rates. This is apart, of course, from the violent contrast in VIII mod., discussed a moment ago.

Otherwise there is marked general agreement at the two sites for all the curves above the *Menyanthes* horizon. This inclines me to think that there is something of genuine significance in the higher NT/T values in the early part of VIII, with its peak value in corresponding positions in the two diagrams and the associated over-emphasis and false maxima in the non-tree pollen curves. If there is a genuine significance we may be dealing with a foretaste, so to speak, of the human activities later so drastically effective in VIII mod. or, on the other hand, the climatic change associated with RY III may well have affected forest density or pollen productivity without upsetting the relative proportions of the tree components. Here again is a problem which is better left open at this stage.

*Earlier stages of the non-tree pollen curves.* Instead of taking the curves individually, they will be used collectively for the basis of a short piece of ecological reconstruction. We begin then on this site with a dense alder-birch woodland whose trees were probably rooted in the mineral soil, and provided more pollen than the ground flora, which consisted mainly of grasses, rushes and ferns. Presently, however (at the stage represented by 340 cm. depth), a change has been completed which has caused the opening out of the woodland to allow a much more luxuriant development of grasses. At this stage the trees were probably rooted in peat. *Juncus* is fading out, and while ferns persist, Ericaceae are rather more frequent and pockets of woodland *Sphagna* are scattered here and there. At length (300 cm. depth) the woodland succumbs to the bog type of vegetation which we may imagine to have been spreading gradually westwards all this time from the more poorly drained central region of the bog. Ferns and grass and woodland *Sphagna* diminish with the retreating woodland, leaving Ericaceae and Cyperaceae as dominants, while bog *Sphagna* come in a little later in frequent patches, though not as dominants. The further development of this bog type is soon, however, rudely interrupted by the



sudden onset of excessively wet conditions which cause persistent shallow pools over the bog surface in which *Menyanthes trifoliata* can flourish. Ericoids give way to moisture-tolerating grasses and we have in fact to envisage a supply of surface water great enough to convert the whole of this lower lying western part of the bog into one great flush area, comparable in its vegetation with the flush region at the north-west corner of the bog, where a few plants of *Menyanthes* still grow to-day.

Presently, however, the violence of the rain abates, *Calluna* returns to its own, *Eriophorum vaginatum* increases, and *Sphagnum* starts on its progress to ever increasing importance and rate of accumulation, until a halt is called by the onset of 'modification'.

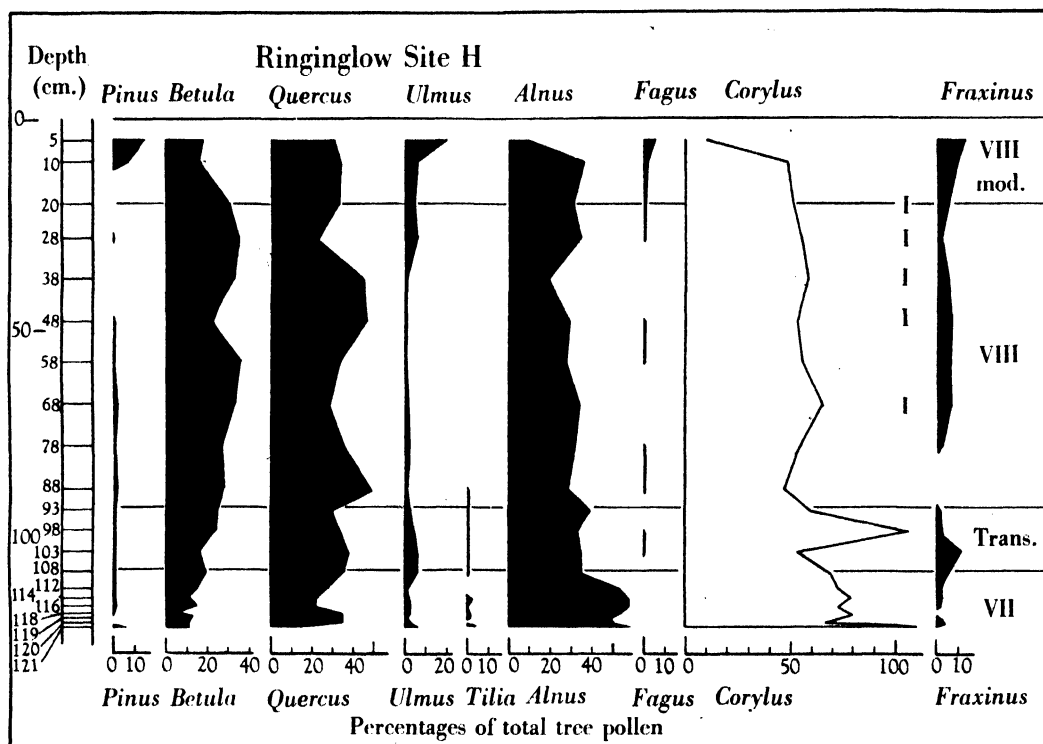


Fig. 10. Pollen diagram for site H. *I.*, *Ilex* pollen. Vertical scale is double that of Figs. 8 and 9.

#### Sites H and D

The gently sloping hillside to the south of the road is covered by peat which is for the most part between 1.0 and 1.5 m. deep. On the north-west and west-facing slopes of this hill the peat is thinner, but has almost certainly been to a great extent destroyed by frequent fires in that area. The peat thins out also around site D, which lies on the watershed between the bog area and the next catchment area to the south. Site H, however, where the peat was 120 cm. deep, was chosen as being likely to give a profile typical of the gentle slopes of this district. The ground is very slightly convex, and the site is well removed from any drainage channel.

The results of pollen analysis at site H are given in Fig. 10, and taken as a whole, the most striking feature is the clear relationship of the diagram with that for site C, even though the peat depth there is five times the depth at site H. There is, however, a difference

It is the *Corylus* curve that shows the closest likeness in the two diagrams and forms the strongest evidence that they both cover the same time period, that is to say, that peat formation at site H began early in zone VIIa. The definition of the time-zones in the site H diagram was less easy than in the longer diagrams. In the first place, it is not clear from the diagram whether or not the whole of zone VIIa is represented by the lowest sample alone. It cannot in any case have covered more than the basal 3 cm. of the profile, to judge by the *Corylus* curve. Then again, there are no *Menyanthes* records by which to place the

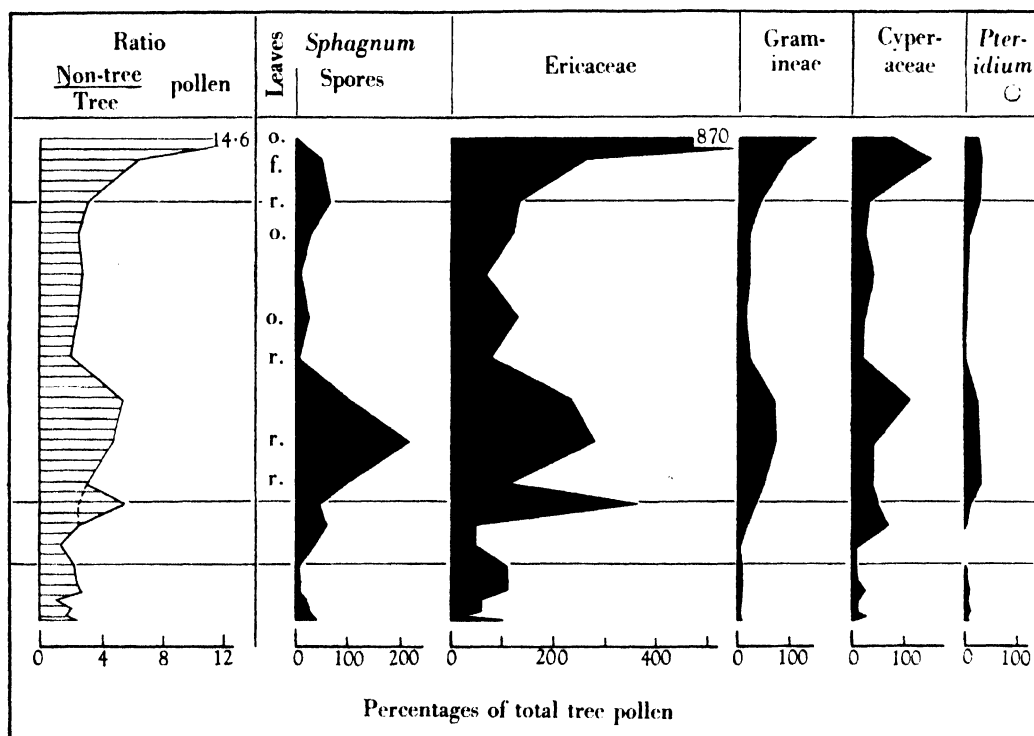


Fig. 10.

Since according to the interpretation here given, zones VII and Transition have suffered relatively so much greater compression than zone VIII, one would expect the T.P.F. to show correspondingly exaggerated values in these early zones. Unfortunately, this diagram was not worked out with the quantitative methods used for sites A and C, but in counting the slides, rough estimates were obtained which fully supported this expectation.

The higher *Pinus* value in the basal sample confirms the conclusion reached from the *Corylus* curve, that peat formation started early in VIIa. It is true that the actual value

(6%) is not high, but the pollen preservation in this sample was poor, and *Pinus* pollen grains always suffer more than those of other trees, so that this must be taken as a minimum value. It must be emphasized that at site C there are no values of *Pinus* higher than 3% between the end of zone VIIa and the beginning of VIII mod.

The *Tilia* values give further confirmation to the conclusion, for it seems to be a general rule in southern Pennine pollen diagrams that *Tilia* values of more than 1% (or very occasionally 2%) do not occur at horizons higher than the base of Transition, except in the extreme surface layers.

Since this site, as already described, may be taken as a fair representative of the shallow peats on gentle slopes, it follows that peat formation began at roughly the same time over practically the whole area under consideration, that is to say, the area indicated in Fig. 1, except for the steeper slopes and projecting summits and ridges. If this interpretation of the site H diagram were not accepted, the only plausible alternative would be to hold that the shallower peats (less than 2 m., say) did not start to form until the onset of wetter

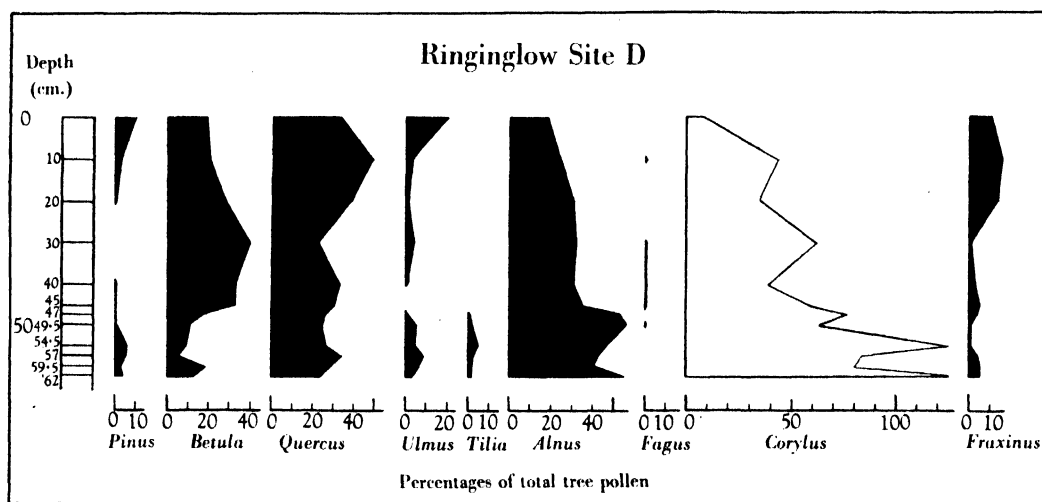


Fig. 11. Pollen diagram for site D. Vertical scale is double that of Figs. 8 and 9.

conditions at the time of the *Menyanthes* horizon. Then presumably the areas now carrying shallower peats would have been forest-clad before that date, and one would expect a sharp change in the NT/T ratio in the diagram for site C at the *Menyanthes* level. The entire absence of any such change gives substantial backing to the conclusion that peat formation was general before the date of the *Menyanthes* horizon, even though in many areas the rate of formation was extremely slow.

Further, these conclusions should resolve a difficulty which was raised by Godwin & Clark (1934) in relation to the blanket peat at Warcock Hill, a locality not more than 25 miles distant from Ringlinglow and in the same type of country. Woodhead & Erdtman (1926) had put forward the view that the base of the Warcock Hill peat was of early Atlantic Age, but this was not acceptable to Godwin & Clark because it had been shown that Bronze Age artefacts were contained in the basal peat layers. There was a depth of 3 ft. of peat at the site which yielded the archaeological data and hence the site is closely comparable with Ringlinglow site H. It will be seen from Fig. 10 that the beginning of

Transition lies at a distance of only 12 cm. (5 in.) from the base of the peat, and since this horizon, as already discussed, is assumed to be dated roughly to 1200 B.C., there is nothing surprising in the fact that Bronze Age implements should be found within 6 in. of the base of the Warcock Hill peat. On the other hand, the results from site H also justify Woodhead & Erdtman in holding that peat formation started at the beginning of Atlantic times. However, the rate of peat formation was so extremely slow to start with that one might more appropriately express the same fact by saying that on areas of small slope and at altitudes over 1000 ft. (300 m.), the general forest cover was destroyed by the changes which took place at the Boreal-Atlantic transition.

The non-tree pollen curves for site H agree well with those for site C except at the base, where there is naturally nothing to represent the 'grassy flush' which characterized zone VIIa at site C. It was clear from numerous trials with the borer around site H, that the original ground surface was irregular and rocky, and the high values for Ericaceae in the basal sample suggest a *Calluna* heath barely clothing a rough hillside of rock and boulders, and this type of vegetation probably continued at this site throughout VII.

The peak value for Ericaceae just at the top of Transition must at present be considered as a purely local effect since there is nothing to correspond with it in the other diagrams. As in similar cases in Fig. 8, a 'corrected' value for the NT/T curve is shown by the dotted lines. For VIII and VIII mod. there is remarkable general agreement between all the non-tree curves and those for sites A and C, and in particular there is confirmation of the difference between the earlier and the later half of VIII. Ericoid values have the higher levels of site A rather than the lower levels of site C, and *Sphagnum* is throughout of lesser importance. The only sample to show any quantity of *Sphagnum* leaves is at 10 cm. depth. A thin layer of fresh *Sphagnum* close to the surface characterizes not only this site, but nearly all the shallow peats of this district.

Finally there are the data shown in Fig. 11 for the short profile at site D. Comparison with Fig. 10 suggests that here again the whole time sequence is covered since the beginning of VII, and that this profile represents the last term in a series showing increasing compression of the time-scale. However, if it were not accepted that this diagram includes zone VII, it would not seriously affect the general conclusions based on site H, since the extent of peat as shallow as that at site D is relatively small in the Ringinglow area. The diagram has therefore been left without zonation, partly because, owing to the compression of the time-scale, the distance between the samples turned out to be too great, so that the diagram is somewhat unsatisfactory and difficult to zone. For the same reason the non-tree curves lack sufficient detail to be of much interest, and are not shown. As far as they go, they fall in with those of Fig. 10.

#### 4. DISCUSSION

The data have been presented in a rather condensed form, and it may be useful to stand back and pick out some of the main conclusions. First, this area shows a depth of peat capable of yielding a detailed record of vegetational changes since the Boreal-Atlantic transition. It is comparable in this respect with lowland raised bogs, which have so far, together with the East Anglian fen peats, received much the greatest weight of attention from British peat investigators.

Secondly, it is comparable again with the lowland types in being essentially a *Sphagnum* bog, thus strongly supporting Pearsall's contention (cf. Pearsall (1941), p. 174) that

present-day blanket peat vegetation is in many places secondary in nature, being derived by the action of biotic, and especially human factors in modifying the natural bog vegetation, of which *Sphagnum* is the dominant.

Thirdly, while a sharp stratigraphical 'Grenz' horizon has not been demonstrated in the field, there is at least one horizon in the bog where the changes shown by detailed investigation are only explicable in terms of a great increase in general wetness. This is the level which has here been called the *Menyanthes* horizon, and is taken, in accordance with Godwin's interpretation, to represent Granlund's RY IV, usually dated about 1200 B.C. The later horizon, RY III, can also be recognized in the data but is even less conspicuous, presumably because at this altitude the degree of climatic wetness needed for rapid bog development was already attained after RY IV so that a further jump in the process of climatic deterioration had relatively little effect.

Godwin has shown that the stratigraphical change from much decayed to fresh *Sphagnum* peat, usually associated with RY III, has sometimes been brought about at an earlier date under appropriate conditions of topography, altitude, or longitude. But numerous observations of peat profiles in the Pennines, especially in shallower peats, have already made it probable that this type of change has also occurred at dates later than that of RY III, and therefore can sometimes be better correlated with RY II or I. One is thus brought to regard the post-atlantic climatic deterioration as consisting of a whole series of rather sudden steps, all roughly in the same direction, rather than as one major step at the time of the main 'Grenz' horizon. The degree and type of response of the vegetation to any one of these steps will depend on a complex of factors, but particularly on those geographical factors just mentioned.

Fourthly, because, in the centre of the bog, growth has continued actively until the last 100 years, and is still continuing at a slow rate, the record of regional forest destruction is shown here by the pollen data in a manner not often attained in this country. It is possible to get some rough idea of the date when this destruction started, that is, the date of the beginning of VIII mod. Such a dating depends on the assumption that the rate of peat growth at site C was approximately the same during the whole period from the beginning of zone VIII until the date of the replacement of *Sphagnum* by *Eriophorum vaginatum*, say not later than A.D. 1850. This assumption is based on the general similarity of peat type—fresh *Sphagnum* peat—throughout the horizons concerned. If the assumption is justified, then

$$\frac{\text{No. of years for VIII mod.}}{\text{No. of years for VIII}} = \frac{\text{Depth of peat for VIII mod.}}{\text{Depth of peat for VIII}},$$

and since, as already discussed, zone VIII is held to start about 500 B.C. that brings the beginning of VIII mod. to about A.D. 1100. This dating is far from rigidly fixed, but is useful as a rough indication. We have noted earlier that the maximum value for NT/T is reached at 38 cm. depth, and on the same type of calculation, this would correspond to a dating of about A.D. 1600, suggesting that the hillside woodlands in this region had already been almost completely destroyed by the seventeenth century.

Finally there is set out in the following table a broad summary of the peat history for the three Ringinglow sites most fully investigated, which may be considered as examples of the three main types of peat deposit in the area, together with the proposed correlations and datings of the various horizons.

VEGETATION AND PEAT CHARACTERS						
ZONE	Site C (600 cm. peat) Trough in original ground surface, but far removed from main drainage system		Site A (400 cm. peat) Always slightly influenced by main drainage system		Site H (120 cm. peat) Sloping hillside, better drained than central bog sites	
VIII mod.	<i>Eriophorum vaginatum</i> dominant	<i>Calluna</i> dominant, <i>Sphagnum</i> unimportant, peat growth very much slower	<i>Calluna</i> dominant	Present surface	A.D. 1946	} Period of <i>Sphagnum</i> loss at site C } Date assumed on general probability } Period of forest destruction in the region } Date calculated from the data for site C
VIII	<i>Sphagnum</i> dominant and fresh, peat growth rapid	<i>Sphagnum</i> dominant, <i>Calluna</i> abundant	Vegetation as below, rate of peat growth slower		A.D. 1850	
			<i>Calluna</i> and <i>Eriophorum vaginatum</i> dominant, <i>Sphagnum</i> rare. Peat growth less slow		A.D. 1100	
Trans.	Changing gradually from the type below to <i>Sphagnum</i> dominance above	Changing from Gramineae with <i>Menyanthes</i> below, to Ericaceae, Cyperaceae and some <i>Sphagnum</i> above			500 B.C.	Granlund's RY III (G.H. of Godwin (1945))
		Bog type, mainly Ericaceae and Cyperaceae, <i>Sphagnum</i> rare	<i>Calluna</i> heath with very slow peat formation, <i>Sphagnum</i> absent	' <i>Menyanthes</i> '	1200 B.C.	
VIIIb	Ericaceae and Cyperaceae dominant, <i>Sphagnum</i> subordinate, peat slow-growing					
VIIa	Gramineae and Cyperaceae dominant, <i>Sphagnum</i> rare, peat amorphous, very slow-growing	Damp <i>Alnus-Betula</i> woodland, forming wood peat. Rate of formation slower in VIIa than in VIIb	<i>Calluna</i> heath, rate of peat formation negligible	<i>Ulmus</i>	3500 B.C.	Date taken from Godwin (1945)
VI	Whole area probably forest clad, with <i>Pinus</i> dominant				B.A.T.	Date taken from Godwin (1945)

## SUMMARY

1. An area of deep blanket peat is described, about 400 acres (1.6 km.<sup>2</sup>) in extent, lying about 6 miles (10 km.) south-west of Sheffield, at an altitude of about 1300 ft. (400 m.). It lies on a very gradual slope with much restricted drainage.

2. Wood peat occurs in the lower layers at the better-drained and more sheltered end of the bog. The main mass of peat has been formed predominantly by *Sphagnum* spp. *Eriophorum vaginatum* has been a constant component of the bog vegetation, but at no time until the present day has it been a dominant.

3. Pollen analysis shows that peat formation began throughout the area at the time of the Boreal-Atlantic Transition (c. 6000 B.C.).

4. Evidence is brought forward of wide-scale destruction of forest in the region, beginning somewhere around A.D. 1100, and continuing to a maximum depletion in the seventeenth century.

I am indebted to the Royal Society for the loan of the peat-borer which was used during this investigation. My warm thanks go to Mr Boulton and Mr Morgan and their students in the Department of Civil Engineering at Sheffield University, for carrying out the hardest part of the surface survey, and to Miss G. Kolisko, of Sheffield University, without whose assistance in the field the laborious work with the peat-borer would have been almost impossible. Lastly, I have had the great advantage of discussing with Professor W. H. Pearsall, Dr H. Godwin and Professor A. R. Clapham, the many problems which have arisen in the course of the work, and to them I wish to express my thanks.

## APPENDIX

*Notes on pollen types not discussed in the main text*

It seems worth recording briefly some data on pollen records which do not at present shed light on the ecology of the bog itself, but which might prove useful in conjunction with any future pollen analytical work on north of England peats. The numbers in the tables are the numbers recorded during the counting of 150 tree pollens in each sample.

*Notes and comments on the tables*

1. *No. of other species.* It must be emphasized that this column deals with species and not with pollen grains. It covers species other than the standard list of trees, *Corylus*, *Fraxinus*, Bryophyta, Ericaceae, Gramineae, Cyperaceae, Ferns and *Pteridium*.

In working through the slides, a note was kept of all pollen grains which were well enough preserved to show their morphology; numbers were given to those whose genus was unknown.

2. *Artemisia vulgaris.* These fossils agree exactly with the pollen of the recent species and are named accordingly, but this type of pollen structure is a frequent one and hence too much weight should not be placed on the identification.

3. *Rumex acetosella.* Exactly the same comment applies here as in the case of *Artemisia vulgaris*.

4. *Composite types (b) and (c)*. These are named after their resemblances to figures in Erdtman (1943); type (b) to his Pl. VIII, fig. 135 (though the fossil is smaller), type (c) to his Pl. VIII, fig. 139. Exact matches for the fossil types have not yet been found.

Table 1. *Site C*

Zone	Sample depth cm.	Total no. of 'other spp.'	Compositae types			<i>Rumex acetosella</i>	<i>Plantago</i> type	<i>Salix</i> type	Cereal type
			<i>a</i> <i>Artemisia vulgaris</i>	<i>b</i> <i>Crepis</i> type	<i>c</i> <i>Bidens</i> type				
VIII mod.	0	18	1	2	1	42	40	4	6
	10	17	2	1	1	14	108	5	12
	22	21	2	2	2	26	104	6	12
	30	12	2	6	5	40	86	1	15
	38	18	3	3	—	22	90	8	9
	46	21	4	1	6	17	96	3	4
	60	13	3	4	3	13	32	2	6
	80	17	2	2	15	5	20	2	8
VIII	100	8	2	—	2	3	5	—	3
	120	11	2	1	2	—	11	—	—
	140	11	2	—	2	—	4	3	2
	160	11	1	—	5	—	6	2	1
	180	10	2	—	1	1	3	5	2
	200	4	1	—	—	—	3	1	—
	220	8	7	—	1	1	12	3	1
	245	15	3	2	—	19	42	5	—
	260	12	1	1	—	2	18	1	1
	280	8	—	—	—	1	18	—	1
	295	11	1	1	—	3	14	3	—
Trans.	310	9	1	—	—	1	7	3	—
	320	7	2	—	—	—	12	—	—
	340	4	—	—	—	2	2	—	—
	360	5	—	—	—	1	3	—	—
	380	10	3	—	—	1	9	2	—
	400	5	—	—	—	1	9	—	—
VII b	420	7	2	—	—	1	5	—	—
	440	5	?	—	—	2	7	—	—
	460	5	—	—	—	—	—	—	—
	480	4	—	—	—	—	1	—	—
	500	5	—	—	—	—	—	—	—
	510	4	1	—	—	—	—	—	—
	520	4	2	—	—	2	—	1	—
	530	4	?	—	—	?	1	—	—
VII a	540	4	—	—	—	—	2	—	—
	550	5	1	—	—	—	—	2	—
	560	4	—	—	—	1	—	—	—
	575	3	—	—	—	—	—	—	—
	585	3	—	—	—	—	—	—	—
	590	5	—	—	—	—	—	—	—
	595	6	—	—	—	—	—	—	—
	600	2	—	—	—	—	—	—	—
VI	605	3	—	—	—	—	—	2	—
	607.5	3	—	—	—	—	—	—	—
	609	4	—	—	—	—	—	1	—

5. *Plantago* type. In view of the findings of Iverson and Godwin\* one would wish for a clear picture of *Plantago lanceolata* pollen frequencies in this northern locality. Unfortunately it is probable that the records here include more than one species owing to rather wide but continuous variation in size and texture. However, any *P. lanceolata*

\* See Godwin, H. *Nature*, **153**, 511, and **154**, 6.



grains that occurred are included in this category and hence the figures give the outside limits for time-range and frequency.

6. *Salicoid*. These records certainly cover more than one *Salix* species, but possibly not more than two. One is larger than any species illustrated by Erdtman, the other is smaller and agrees with *S. atrocinerea*.

Table 2. Site A

Zone	Sample depth cm.	Total no. of 'other spp.'	Compositae types			<i>Rumex acetosella</i>	<i>Plantago</i> type	<i>Salix</i> type	Cereal type
			a <i>Artemisia vulgaris</i>	b <i>Crepis</i> type	c <i>Bidens</i> type				
VIII mod.	0	14	3	—	—	21	17	1	—
	10	13	3	2	5	3	44	1	21
	20	13	1	2	—	8	14	1	3
	30	9	—	1	1	3	6	2	—
	40	7	3	—	—	1	3	4	—
VIII	55	8	3	—	4	8	6	3	1
	70	10	6	—	1	5	6	1	—
	85	6	1	1	—	2	2	2	—
	100	5	—	—	—	2	2	—	—
	120	8	1	1	—	3	6	4	—
	140	10	2	2	1	9	31	4	1
	155	5	3	—	—	15	25	1	1
	175	9	—	1	1	4	9	—	—
	195	7	1	—	—	4	6	1	—
	215	6	2	—	—	2	4	—	—
Trans.	225	5	1	—	—	1	7	1	—
	235	7	2	—	—	3	4	2	—
	255	6	—	—	—	15	18	2	—
	275	3	—	—	—	31	—	1	—
	295	4	1	—	—	5	2	2	—
VII b	315	6	—	—	—	5	5	22	—
	335	4	—	—	—	3	—	1	—
	345	1	—	—	—	—	—	—	—
	355	1	—	—	—	—	—	1	—
	365	2	—	—	—	—	1	—	1
	370	3	—	—	—	—	—	1	—
	375	0	—	—	—	—	—	—	—
	380	1	—	—	—	—	1	—	—
	385	2	—	1	—	—	5	—	—
	390	0	—	—	—	—	—	—	—
VII a	392.5	0	—	—	—	—	—	—	—
	395	2	—	—	—	—	2	—	—
	397.5	0	—	—	—	—	—	—	—
	400	1	—	—	—	—	1	—	—
	402.5	1	—	—	—	—	—	—	—
	405	0	—	—	—	—	—	—	—
	407.5	1	—	—	—	—	—	—	—

7. *Cereal pollen*. Gramineaceous pollen of double or more the average size was noted and is provisionally attributed to cereal species. Its marked increase in VIII mod. is obviously significant.

8. *General features of the tables*. Both tables show an increase both in variety of types, and of numbers of grains within each type, in passing upwards from the base. There is good agreement between the two tables in the general drifts of the numbers, especially after the end of the woodland phase at site A. Broadly, the drifts are the same as those shown by the non-tree pollen types plotted in Figs. 8 and 9.

*Additional Notes*

*Juncus pollen*. Large numbers of Juncaceous tetrads were found at 180 cm. in site C, though none was found at levels containing *Juncus* seeds. This delicate pollen is clearly not preserved under conditions of high humification but must be able to survive sometimes in rapidly growing peat.

*Juglans type*. One grain at 45 cm., site C.

*Acer pseudoplatanus*. Surface samples, sites A and C.

? *Sorbus aucuparia*. Surface and 20 cm., site A.

*Galium saxatile*. A few grains, all occurring above the VIIa-VIIIb horizon.

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## THE VEGETATION OF THE ISLANDS OF CANNA AND SANDAY, INVERNESS-SHIRE

By G. F. ASPREY

*(With Plates 4 and 5 and two Figures in the Text)*

Some information on the natural history of the islands of Canna and Sanday has been given by Bertram (1939) while Harrison (1939) has produced a flora for these and other Hebridean islands. A party from Glasgow University visited the islands in 1938 and 1939 and the data on which the present account is based were gained partly during these visits and partly as a result of observations made by the author in 1940.

The islands of Canna and Sanday are situated approximately 8 miles south-west of Skye, being part of a group comprising the Small Isles Parish of Inverness-shire. They are included in the vice-county 104 of the Watson Topographical Divisions. Canna has lying near to its south-east shore the smaller island of Sanday (see Map, p. 185), and their proximity provides a good natural harbour. Canna is about  $4\frac{1}{2}$  miles (7.2 km.) long, running from east to west, and on the average about a mile (1.6 km.) wide. Sanday is almost 2 miles long (3.2 km.) and varies from a furlong (0.2 km.) to  $\frac{3}{4}$  mile (1.2 km.) in breadth covering an area of about 1 sq. mile (256 hectares). The geology of the islands has been described by Harker & Barrow (1908) as consisting almost entirely of volcanic rocks in which columnar basalts, dolerites and agglomerates are conspicuous. These may be seen both as outcrops of dolerite sills and as fine natural sections presented by the cliffs. Canna is divided into an eastern and a western half by a relatively broad depression at Tarbert where the island is only  $\frac{1}{2}$  mile wide. The western plateau averages 400 ft. (122 m.) above sea-level and this height is maintained along the southern boundary. In the north and north-west, however, the plateau slopes down gradually to cliffs of 100 ft. (30.5 m.) and thence to a coastal ledge of varying width. On the eastern plateau the highest points lie near the northern shore [Beinn Tighe 550 ft. (168 m.), Càrn a Ghaill 690 ft. (210 m.)] resulting in almost vertical cliffs up to 550 ft. high. This plateau slopes more gradually to the south where the coastal ledge is reached from a height of 250 ft. (76 m.) by means of steep grassy slopes in the east above A Chill and An Coroghon or by cliffs and boulder-strewn slopes from Ealaist westwards. At Tarbert and between Rudha Dubh and An Coroghon the best farmland is found situated on raised beaches. With the exception of the coastal ledges and the north shore of the Tarbert depression the islands are almost entirely cliff bound. The cliffs are very precipitous and for the most part inaccessible. The highest ground on Sanday is situated near the southern shore where the cliffs average 50 ft. (15 m.) in height reaching a maximum of 100 ft. near the highest point in the island Tallabric 193 ft. (58 m.). For the most part the ground slopes towards Canna's harbour and the northern shore. Several crofts are to be found around the large bay opposite Canna.

The extent of the enclosed meadow and arable land is indicated on the map and comprises altogether upwards of 190 acres (76 hectares). Before the introduction of sheep

much more land was under cultivation, 460 acres (184 hectares) in 1805; these areas now support grassland.

The islands experience a rainfall of 50–60 in. (125–160 cm.) per annum and are subject to strong winds and gales. Although no precise meteorological data are available the number of cloudy and rainy days is large in this area and a humid atmosphere prevails. The temperature range is from 41° F. (mean January) to 56° F. (mean July) and is only exceeded for rare brief periods.

The climate, topography and grazing by sheep and rabbits seem to be the main factors affecting the distribution of the vegetation. Grassland, occasionally interrupted by *Calluna* heath or patches of bracken, extends up the slopes leading to the high ground of Canna and over most of Sanday. Moorland vegetation covers the plateaux of Canna and is characterized by the presence of caespitose and oxyphilous plants among which *Scirpus caespitosus*, *Molinia coerulea* and *Calluna vulgaris* are conspicuous (see Fig. 1). No natural

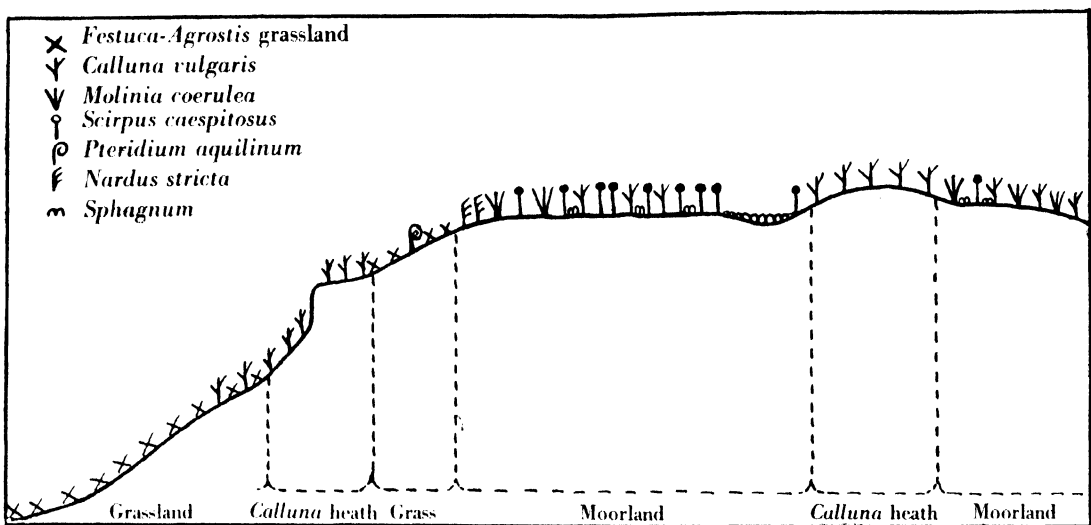


Fig. 1. Diagram showing the distribution of the main communities on Canna in relation to topography.

woodland occurs, but the possibility of tree growth in the more sheltered parts is shown by the plantations of pine, larch and sycamore which occur near Canna House and in the gully at An Coroghon (see Map, p. 185). For a description of these plantations reference may be made to Bertram (1939). The natural vegetation of the islands may be conveniently considered under the following headings:

- I. Canna harbour and the maritime vegetation.
- II. The sea-cliff vegetation.
- III. The grassland and *Calluna* heath.
- IV. The moorland.
- V. The flushes and water courses.

#### I. CANNA HARBOUR AND THE MARITIME VEGETATION

The maritime communities are confined, for the most part, to the sheltered harbour and its vicinities where three types of habitat may be distinguished.

*(a) On volcanic agglomerate and shingle*

The most conspicuous feature of the harbour vegetation is the sea-turf community developed intermittently as a narrow belt, under tidal influence, on the volcanic agglomerate and more stable shingle. It is characterized by an abundance of compact rosettes of *Armeria maritima* and *Plantago maritima* with tufts of *Glyceria maritima*, and has the following composition:

	<i>Armeria maritima</i>	c.d.	
	<i>Glyceria maritima</i>	c.d.	
<i>Atriplex hastata</i>	o.	<i>Plantago coronopus</i>	o.
<i>Cochlearia officinalis</i>	o.	<i>P. maritima</i>	s.
<i>Festuca rubra</i> var. <i>glaucescens</i>	o.	<i>Spergularia marginata</i>	o.
<i>Glaux maritima</i>	f.	<i>Suaeda maritima</i>	o.
<i>Juncus Gerardi</i>	l.f.	<i>Triglochin maritima</i>	o.

The turf is 8–12 in. (20–30 cm.) above the level of the rock and seems to be undergoing erosion on the Canna shore with the consequent production of clumps of turf separated by areas of bare rock.

In the large bay on the southern shore of Sanday near Ant Oban an intensively grazed sea-turf community dominated by *Glyceria maritima* is to be found. This plant forms a very dense sward studded with short compact tufts of *Armeria maritima* and less frequently *Plantago maritima*.

*(b) On silt*

A noteworthy modification of the shore vegetation occurs west of Square Farm where there is a considerable deposition of silt between raised clumps of maritime turf. Above a *Pelvetia canaliculata* zone the mud is colonized by *Salicornia europaea* with *Glyceria maritima* and *Armeria maritima* coming in higher up. It seems possible that the sequence of colonization may also be in this order.

*Salicornia* is also present on intermittent deposits of silt along the Sanday shore. Local variation is brought about where brackish conditions are produced by the entry of small streams round the mouths of which it is common to find *Scirpus maritimus*, *Carex vulpina*, *Scirpus rufus* and *Juncus Gerardi*.

*(c) On sand*

Sand deposits occur in the bays at Tarbert, An Coroghon, and more extensively at the north-west of Sanday. The latter is the only one that supports typical sand communities. Here, a relatively large bay of white calcareous sand is surrounded by steep sandy banks leading up to meadowland developed on stable sand from which the following list was taken:

<i>Achillea millefolium</i>	f.	<i>Plantago lanceolata</i>	f.
<i>Agrostis alba</i>	f.	<i>Polygala vulgaris</i>	o.
<i>A. vulgaris</i>	f.	<i>Primula vulgaris</i>	o.
<i>Anthyllis vulneraria</i>	o.	<i>Prunella vulgaris</i>	o.
<i>Arrhenatherum avenaceum</i>	o.	<i>Ranunculus acris</i>	f.
* <i>Avena pubescens</i>	r.	* <i>R. bulbosus</i>	o.
<i>Bellis perennis</i>	f.	<i>Rhinanthus minor</i>	o.
<i>Carex arenaria</i>	o.	<i>Rumex acetosa</i>	o.
<i>Centaurea nigra</i>	f.	<i>Salix repens</i>	l.f.
<i>Cynosurus cristatus</i>	o.-f.	<i>Scabiosa succisa</i>	o.
* <i>Daucus carota</i>	o.	<i>Sedum acre</i>	l.f.
<i>Euphrasia officinalis</i>	l.f.	<i>Senecio jacobea</i>	l.f.
<i>Festuca rubra</i> var. <i>glaucescens</i>	s.	<i>Taraxacum vulgare</i>	o.
* <i>Galium verum</i>	o.	* <i>Thalictrum dunense</i>	f.
<i>Holcus lanatus</i>	o.	* <i>Thymus serpyllum</i>	f.
* <i>Linum catharticum</i>	o.	<i>Trifolium pratensis</i>	f.
<i>Lolium perenne</i>	o.	<i>T. repens</i>	s.
* <i>Lotus corniculatus</i>	f.		

\* Plants characteristic of grassland developed on chalk and basic igneous rocks.

The slopes forming the margin of the bay are from 6 to 10 ft. (180–300 cm.) high and are at an angle of approximately  $55^\circ$ . These banks are dotted with clumps of eroded meadow vegetation, which have been undermined by the agency of the wind and sea. They are separated from one another by mobile sand which in some parts is being recolonized by *Agropyron junceum*, *Carex arenaria*, *Sedum acre*, *Senecio Jacobaea* and *Thalictrum dunense*.

Colonizing the strand immediately below the banks, where there is organic debris washed up by the sea, are open communities of *Arenaria peploides*, *Potentilla anserina*, *Atriplex hastata*, *Rumex crispus* and *Agrostis alba*. These foreshore communities are by no means permanent owing to the severe storms which occur and completely alter the appearance of the bay from time to time as far as the vegetation is concerned.

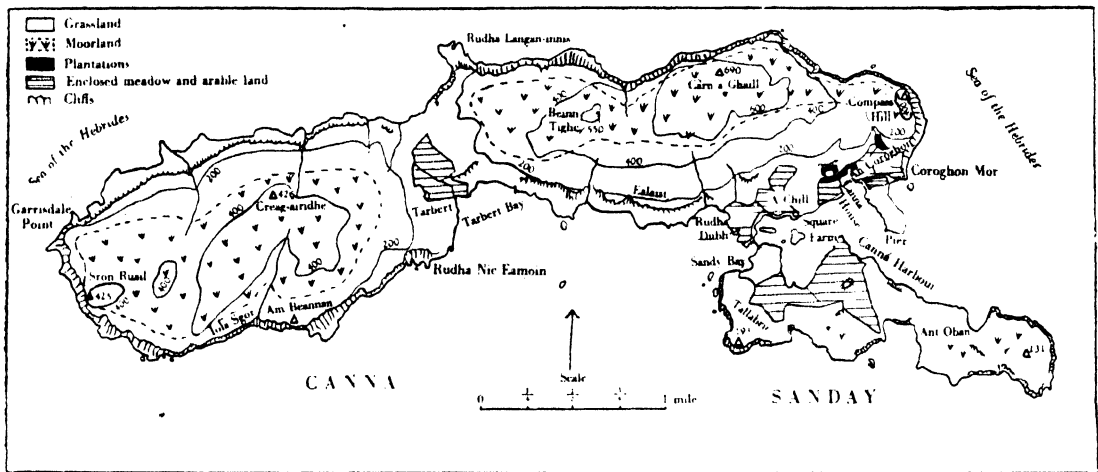


Fig. 2. The islands of Canna and Sanday, Inverness-shire, showing the approximate distribution of grassland and moorland. Contours and spot heights in feet.

Only at one point is there any indication of plant succession. This occurs at the eastern end where one finds a gently sloping area of stable sand, from 1 to 2 ft. (30–60 cm.) above the level of the strand, supporting a more or less closed community dominated by the moss *Tortula ruraliformis* and having the following composition:

<i>Tortula ruraliformis</i> dom.			
<i>Achillea millefolium</i>	o.	<i>Plantago coronopus</i>	o.
<i>Agrostis alba</i>	f.	<i>P. lanceolata</i>	o.
<i>Bellis perennis</i>	o.	<i>Sedum acre</i>	o.
<i>Centaurea nigra</i>	r.	<i>Senecio Jacobaea</i>	o.
<i>Festuca rubra</i> var. <i>glaucescens</i>	a.	<i>Thalictrum dunense</i>	o.
<i>Galium verum</i>	o.	<i>Trifolium repens</i>	o.
<i>Lotus corniculatus</i>	l.f.		

Towards the strand the vegetation becomes more open and the only plants to be seen are *Arenaria peploides*, *Glaux maritima*, *Potentilla anserina* and *Sedum acre*. At the extreme edge of the strand where the sand is extremely mobile *Arenaria peploides* and *Carex arenaria* are the sole occupants. It seems very probable that these two plants are pioneers, as they withstand inundation by blown sand since they are able to grow through it. They tend to form a more stable substratum above the general level of the bay and this action is encouraged in this particular area owing to there being a certain amount of protection afforded from wind and wave action. At this stage *Tortula* comes in and further

consolidation and building up follows with subsequent invasion by the other species mentioned in the list. From here it is but a short step to the formation of the meadowland most members of which could be found round the landward margin of the community.

## II. THE SEA-CLIFF VEGETATION

The vegetation of the sea cliffs shows considerable variation as the result of the operation of such factors as slope, exposure and altitude. The most exposed cliffs are in the west and south-west extending from Garrisdale Point to Rudha Nic Eamoin. Here they average 400 ft. (122 m.) in height and steep, in places vertical, cliffs give way to boulder-strewn grassy escarpments, sloping at angles of 45–50°, which may or may not run down to a coastal ledge. Plant life on such exposed rock faces is confined to crevices where some degree of shelter is afforded. The plants found are a mixture of arctic alpine and halophytic types such as the following: *Silene acaulis*, *S. maritima*, *Sedum roseum*, *Matricaria inodora* var. *maritima*, and *Juniperus sibirica*. The latter may grow out over the cliff edge once it has become firmly established. *Thymus serpyllum* together with a mixture of the grassland species are to be seen on ledges where soil and detritus can accumulate. The crevices and ledges at lower altitudes support the following species in addition to the above:

<i>Anthyllis vulneraria</i>	<i>Ligusticum scotticum</i>
<i>Armeria maritima</i>	<i>Plantago coronopus</i>
<i>Asplenium marinum</i>	<i>P. maritima</i>
<i>Cochlearia officinalis</i>	<i>Sedum anglicum</i>
<i>Hedera helix</i>	<i>Solidago virgaurea</i>

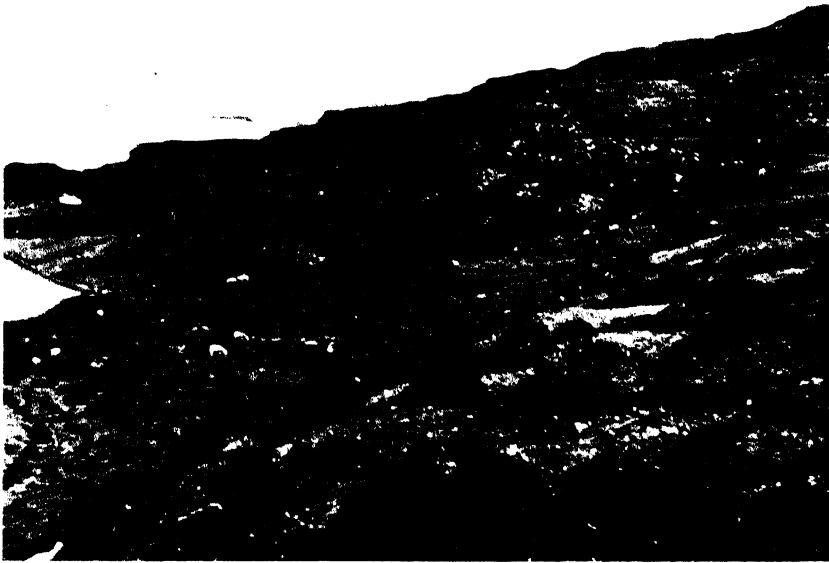
The cliffs in the north-east of Canna from Rudha Langan-innis to Coroghon Mor reach a height of 550 ft. (168 m.). They are somewhat protected from the full force of the south-west gales and are frequented by colonies of sea birds. These two factors may account for the more luxurious vegetation supported in the crevices, on ledges and on the grass slopes protruding from the rock faces. With the possible exception of *Anthyllis* all the species already mentioned are to be found here, and in addition there exists on the ledges a great variety of plants mixed with grassland species. The most interesting of these are the woodland and shade-loving types such as *Angelica sylvestris*, *Athyrium filix-femina*, *Blechnum spicant*, *Lonicera periclymenum*, *Luzula sylvatica*, *Valeriana officinalis* and *Oxalis acetosella*. For the most part these plants are only found in this habitat on the island and it is worthy of note that Petch (1933) has reported a similar mixture for the high cliffs at St Kilda. Conditions on some of the ledges must closely approximate to woodland. The plants will rarely be exposed to direct sunlight, humid conditions prevail and the soil is fertile since all types grow luxuriantly. They may have spread here when the island was still supporting some natural woodland (see p. 192).

At the top of the sea cliffs on Sanday it was common to find rock detritus supporting open communities of *Plantago coronopus*, *P. maritima*, *Armeria maritima* and *Koeleria cristata*. The three former plants were in the form of rosettes from 1.5 to 5 cm. in diameter and 1.5 cm. high. The plants were closely cropped by rabbits and in addition were subject to extreme exposure to wind and sea spray. Similar communities have been reported by Praeger for corresponding situations in Ireland (1911, 1934). On the high cliffs of Canna, where sea spray cannot reach, such areas are mainly colonized by *Koeleria*.

The grassy escarpments below the rock faces on the high cliffs of Canna consist of a *Festuca-Agrostis* community similar to that to be described in the next section. The grasses







Phot. 1. The effect of grazing on the *Calluna* heath situated on the steeper slopes above A Chill.



Phot. 2. The approaches to the eastern plateau of Canna as seen from near Compass Hill looking north-west towards Càrn a Ghaill. A *Sphagnum* bog is to be seen in the foreground followed by a succession of mounds and rock outcrops covered by *Festuca-Agrostis* grassland and *Calluna* heath (dark patches) with an admixture of moorland species.

### III. THE GRASSLAND AND *CALLUNA* HEATH

(a) *Festuca-Agrostis grassland*

<i>Agrostis vulgaris</i>	a.-l.d.	<i>Prunella vulgaris</i>	o.
<i>A. canina</i>	f.-l.a.	<i>Pteris aquilina</i>	o.
<i>Anthoxanthum odoratum</i>	f.	<i>Rumex acetosa</i>	o.
<i>Arrhenatherum avenaceum</i>	o.	<i>Scabiosa succisa</i>	f.
<i>Calluna vulgaris</i>	l.f.	<i>Sielingia decumbens</i>	o.-l.f.
<i>Carex panicea</i>	l.f.	<i>Teucrium scorodonia</i>	o.
<i>Cynosurus cristatus</i>	r.	<i>Thymus serpyllum</i>	r.
<i>Euphrasia officinalis</i>	f.	<i>Trifolium repens</i>	o.-l.f.
<i>Festuca ovina</i>	a.	<i>Viola riviniana</i>	f.
<i>F. vivipara</i>	o.		
<i>Galium saxatile</i>	f.	<i>Mosses</i>	
<i>Holcus lanatus</i>	l.f.	<i>Brachythecium purum</i>	} Common ground flora
<i>Koeleria cristata</i>	o.	<i>Hypnum cupressiforme</i>	
<i>Lathyrus pratensis</i>	o.	<i>H. schreberi</i>	
<i>Lotus corniculatus</i>	l.f.	<i>Hylocomium splendens</i>	
<i>Luzula campestris</i>	f.	<i>Thuidium tamariscinum</i>	
<i>Potentilla erecta</i>	l.f.		

In the sheltered north-eastern sides of exposed knolls and outcrops, a 'lair' flora is developed whose lush green colour is in marked contrast to the drab tones of the rest of the vegetation. Animals regularly shelter in such places and the intensive grazing and manuring has produced a short green *Agrostis* turf whose composition is in the main similar to the above. *Calluna* and *Arrhenatherum* were, however, absent while *Plantago lanceolata*, *Achillea millefolium* and *Cerastium vulgatum* were common.

\* The pH determinations were made on the spot by the aid of a B.D.H. soil-testing outfit, and they must be considered as approximate only.

(b) *Calluna heath*

*Calluna* heath occurs on steep boulder-strewn escarpments leading up to rock outcrops and on steep slopes and mounds leading up to and on the plateaux (see Fig. 1 and Pl. 4, photos. 1, 2). The soil is generally shallow and stony underlying a surface layer of raw humus although in flatter areas it may be deeper and podsolized. The *Calluna* is kept short by grazing and, in some areas, by burning as well. There is no doubt that these two factors prevent *Calluna* heath from spreading to those parts now occupied by grassland, they may also account for the large admixture of grasses. The species consistently found are shown in the following list:

	<i>Calluna vulgaris</i>	dom.	
<i>Agrostis vulgaris</i>	f.	<i>Hypericum pulchrum</i>	o.
<i>A. canina</i>	o.	<i>Lathyrus pratensis</i>	o.
<i>Anthoxanthum odoratum</i>	o.	<i>Lotus corniculatus</i>	o.-f.
<i>Carex binervis</i>	f.	<i>Polygala vulgaris</i>	r.
<i>C. panicea</i>	o.	<i>Potentilla erecta</i>	f.
<i>Erica cinerea</i>	o.-l.a.	<i>Scabiosa succisa</i>	o.
<i>Euphrasia officinalis</i>	o.	<i>Silene decumbens</i>	o.
<i>Festuca ovina</i>	f.	<i>Thymus serpyllum</i>	r.
<i>Galium saxatile</i>	f.	<i>Viola riviniana</i>	o.

and a ground flora of the mosses:

<i>Brachythecium purum</i>	<i>Hylocomium splendens</i>
<i>Hypnum schreberi</i>	<i>Thuidium Tamariscinum</i>
<i>H. cupressiforme</i>	

On the tops of rock outcrops *Calluna* and *Erica* may almost exclude other species. On Sanday *Antennaria dioica* and *Salix repens* are found in addition to the above.

## IV. THE MOORLAND

What may be popularly termed 'moorland' vegetation occurs on the plateaux of Canna and intermittently on Sanday (see Map and Fig. 1). It is confined to areas where the ground is relatively flat so that the drainage is poor. Moreover, a shallow surface layer of peat retards surface drainage so that in this type of climate, where a relatively high rainfall is combined with low evaporation, surface water is frequent and everywhere is a permanently wet peaty soil. The pH value taken at the surface was found to vary between 4.0 and 5.5. As far as the vegetation is concerned there is no general dominant, but for the most part a varying mixture of the following oxyphilous and caespitose types characterizes the area as a whole: *Scirpus caespitosus*, *Molinia coerulea*, *Calluna vulgaris*, with a ground flora of mosses in which *Sphagnum* spp. are conspicuous. Such species are common inhabitants of blanket bog and indeed the climate might lead one to expect this type of 'moorland' vegetation in these islands. It would seem to correspond to the *Scirpus* climatic moor of Fraser (1933) which Tansley (1939) includes in his description of blanket bog. Tansley describes it as the climatic climax in regions of high rainfall combined with high atmospheric humidity with the proviso that the ground is flat or sloping at an angle of not more than 15°, so that the drainage is not free. These conditions apply here for the most part and typical communities to be met with will now be described in more detail.

On the flat areas, which include most of the western plateau, there is to be found a community dominated by *Scirpus caespitosus* and *Calluna vulgaris*. The surface layer of peat may be up to 12 in. (30 cm.) thick covering a water-logged peaty soil up to 2 ft.

(60 cm.) in depth. The *Scirpus* is tufted and is typically scattered with open patches of *Calluna* although either may be locally dominant. The *Calluna* is usually restricted to a height of 6 in. (15 cm.) by grazing. The *Sphagnum* species noted in the list were common, although their relative frequency was not determined they were mostly short forms and hummock formation was only local. *Campylopus atrovirens* is common as well as *Rhacomitrium lanuginosum* and the usual heath mosses. Shallow pools containing *Potamogeton polygonifolius*, *Menyanthes trifoliata* and *Ranunculus flammula* are frequent. The list which follows includes the most consistently occurring species.

	<i>Scirpus caespitosus</i>	} dom.		
	<i>Calluna vulgaris</i>			
<i>Agrostis canina</i>	o.		<i>Festuca ovina</i>	o.
<i>A. vulgaris</i>	o.		<i>Juncus squarrosus</i>	l.f.
<i>Anthoxanthum odoratum</i>	o.		<i>Molinia coerulea</i>	l.f.
<i>Carex echinata</i>	o.		<i>Nardus stricta</i>	o.
<i>C. panicea</i>	o.-l.f.		<i>Narthecium ossifragum</i>	f.
<i>C. pulicaris</i>	o.		<i>Pinguicula lusitanica</i>	r.
<i>Drosera rotundifolia</i>	o.		<i>P. vulgaris</i>	o.
<i>Empetrum nigrum</i>	r.		<i>Polygala vulgaris</i>	o.
<i>Erica cinerea</i>	f.		<i>Potentilla erecta</i>	f.
<i>E. tetralix</i>	l.f.		<i>Scabiosa succisa</i>	o.
<i>Eriophorum angustifolium</i>	l.f.			
<i>Mosses</i>				
<i>Aulacomium palustre</i>	l.f.		<i>Hypnum revolvens</i>	f.
<i>Brachythecium purum</i>	f.		<i>H. schreberi</i>	f.
<i>Breutelia arctuata</i>	l.f.		<i>Leucobryum glaucum</i>	o.
<i>Campylopus atro-virens</i>	l.a.		<i>Rhacomitrium lanuginosum</i>	l.f.
<i>C. flexuosus</i>	f.		<i>Sphagnum acutifolium</i>	a.
<i>Hylocomium loreum</i>	o.		<i>S. compactum</i>	} a.
<i>H. splendens</i>	f.		<i>S. cymbifolium</i>	
<i>Hypnum cupressiforme</i>	f.		<i>S. papillosum</i>	
<i>H. cuspidatum</i>	o.		<i>S. recurvum</i>	

Two other communities met with are marginal to the *Scirpus-Calluna* moorland. The first one to be dealt with corresponds to Fraser's transition vegetation from grassland to moorland. It is to be found above the *Festuca-Agrostis* grassland on wet slopes and is characterized by an abundance of short *Molinia* tufts with *Scirpus caespitosus* coming in on the wetter parts, while *Nardus stricta* often occupies the drier areas. *Calluna vulgaris* is only occasionally present and may be quite absent over relatively large tracts.

	<i>Scirpus caespitosus</i>	} dom.		
	<i>Molinia coerulea</i>			
<i>Agrostis canina</i>	f.		<i>Juncus squarrosus</i>	l.f.
<i>A. vulgaris</i>	f.-l.a.		<i>Nardus stricta</i>	l.a.
<i>Anthoxanthum odoratum</i>	o.		<i>Narthecium ossifragum</i>	f.
<i>Calluna vulgaris</i>	o.-r.		<i>Potentilla erecta</i>	f.
<i>Carex binervis</i>	f.		<i>Scabiosa succisa</i>	o.
<i>C. echinata</i>	f.			
<i>C. pulicaris</i>	f.		<i>Mosses</i>	
<i>Erica tetralix</i>	l.f.		<i>Brachythecium purum</i>	f.
<i>Eriophorum angustifolium</i>	o.-l.a.		<i>Hylocomium splendens</i>	f.
<i>Festuca ovina</i>	f.-l.a.		<i>Hypnum schreberi</i>	f.
<i>F. vivipara</i>	f.		<i>Sphagnum</i> spp.	a.
<i>Holcus lanatus</i>	o.			

The other moorland community is the only one represented on Sanday and would seem to correspond to the *Scirpus-Calluna-Molinia* moor of Fraser (1933) who regards it as a transitional community between *Calluna* heath and the climax *Scirpus-Calluna* moor. In the examples examined in these islands *Scirpus caespitosus* although common was not

thought to attain the status of dominance. Short and diffuse tufts of *Molinia* and *Calluna* are more conspicuous than *Scirpus*. There is a large admixture of heath and moorland species in general although *Calluna* or *Molinia* may be locally dominant.

	<i>Calluna vulgaris</i>	dom.	
	<i>Molinia coerulea</i>		
<i>Agrostis canina</i>	o.	<i>Festuca ovina</i>	o.-l.f.
<i>A. vulgaris</i>	l.f.	<i>F. vivipara</i>	f.
<i>Anthoxanthum odoratum</i>	o.	<i>Holcus lanatus</i>	o.
<i>Carex binervis</i>	f.	<i>Juncus communis</i>	o.
<i>C. echinata</i>	f.	<i>J. squarrosus</i>	l.f.
<i>C. flava</i>	o.	<i>Nardus stricta</i>	l.f.
<i>C. panicea</i>	l.f.	<i>Narthecium ossifragum</i>	f.
<i>Erica cinerea</i>	o.	<i>Pedicularis sylvatica</i>	o.
<i>E. tetralix</i>	l.f.	<i>Potentilla erecta</i>	f.
<i>Eriophorum angustifolium</i>	l.f.	<i>Scabiosa succisa</i>	o.
<i>Euphrasia officinalis</i>	o.	<i>Scirpus caespitosus</i>	f.-l.a.
<i>E. vaginatum</i>	o.	<i>Sielingia decumbens</i>	o.
<i>Mosses</i>			
<i>Brachythecium purum</i>	f.	<i>Hypnum schreberi</i>	a.
<i>Brutelia arctuata</i>	f.	<i>Hylocomium splendens</i>	a.
<i>Hypnum cupressiforme</i>	f.	<i>Sphagnum</i> spp.	a.

According to Fraser both grazing and burning, which in a drier climate would favour the spread of grassland, in moorland areas of this kind encourage the spread of caespitose plants. At Inverliver forest in Argyllshire he was able to distinguish transition types of vegetation, floristically similar to the last two types dealt with above, which he considers will eventually culminate in *Scirpus-Calluna* moorland, the climatic climax type. More evidence would be necessary before it was possible to deduce such stages of succession on these islands with certainty.

One notable feature was the prevalence of *Carex panicea* on sheep tracks wherever they occurred on the moorland. This would seem to show that this plant can withstand the frequent treading of animal hooves and is similar in this respect to *Poa pratensis* reported by Bates (1935, 1938).

In wet depressions on the moorland and its approaches *Sphagnum* bogs are to be found especially in the eastern half of Canna. The larger examples examined all showed drainage channels (Pl. 4, phot. 2; Pl. 5, phot. 3), but they are not very effective having been allowed to become blocked by vegetation with the result that they present, for the most part, the same features as undrained bogs, an example of which may be seen in Pl. 5, phot. 4. The species of *Sphagnum* found included the hummock formers *S. plumulosum*, *S. papillosum* and *S. acutifolium* group together with *S. compactum*, *S. recurvum*, *S. cymbifolium*. These Sphagna, the relative frequency of which was not recorded, form a matrix in which other plants develop, as well as hummocks (Pl. 5, phot. 4) on the top of which *Eriophorum angustifolium*, *Erica tetralix* and *Calluna vulgaris* are to be found. The vegetation of the blocked drains is worthy of comment. In one bog (Pl. 4, phot. 3) *Schoenus nigricans* was predominant while in another *Carex ampullacea* performed a similar role. It was more usual, however, to find the drains occupied by a mixture of *Carex vulgaris*, *Juncus articulatus* and *Eleocharis palustris* with *Ranunculus flammula*, *Menyanthes trifoliata* and *Potamogeton polygonifolius* common in areas of standing water. The following general list has been compiled from several bogs examined:

	<i>Sphagnum</i> spp.	dom.	
† <i>Agrostis vulgaris</i>	o.	<i>Juncus squarrosus</i>	l.f.
† <i>Calluna vulgaris</i>	o.-l.f.	<i>Luzula campestris</i>	o.
* <i>Carex ampullacea</i>	l.a.	<i>L. multiflora</i>	o.
<i>C. dioica</i>	r.	* <i>Menyanthes trifoliata</i>	l.f.
<i>C. echinata</i>	o.	<i>Molinia coerulea</i>	f.
<i>C. flava</i>	o.-f.	<i>Narthecium ossifragum</i>	o.-l.f.
<i>C. panicea</i>	o.	<i>Orchis maculata</i>	o.
<i>C. pulicaris</i>	o.	<i>Pedicularis sylvatica</i>	o.
* <i>C. vulgaris</i>	l.a.	<i>Pinguicula lusitanica</i>	o.
* <i>Comarum palustre</i>	o.	<i>P. vulgaris</i>	o.
<i>Drosera rotundifolia</i>	o.	<i>Polygala vulgaris</i>	o.
<i>Eriophorum angustifolium</i>	l.a.	* <i>Potamogeton polygonifolius</i>	l.f.
<i>Erica tetralix</i>	l.f.	† <i>Potentilla erecta</i>	o.
* <i>Eleocharis palustris</i>	l.f.	* <i>Ranunculus flammula</i>	l.f.
* <i>E. multicaulis</i>	o.	† <i>Rhinanthus minor</i>	o.
† <i>Festuca ovina</i>	o.	† <i>Scabiosa succisa</i>	o.
† <i>Galium saxatile</i>	o.	* <i>Schoenus nigricans</i>	l.a.
† <i>Holcus lanatus</i>	o.	<i>Scirpus caespitosus</i>	o.-l.f.
* <i>Juncus articulatus</i>	l.f.	* <i>S. fluitans</i>	r.
<i>J. bulbosus</i>	o.-l.f.	* <i>Utricularia intermedia</i>	f.
* <i>J. communis</i>	o.		

\* Drains and standing water.

† Drier areas.

It is perhaps noteworthy that neither *Vaccinium myrtillus* nor *Myrica gale* was found on either of the islands although both have been recorded by Harrison (1939).

## V. THE VEGETATION OF THE FLUSHES AND WATER COURSES

### (a) *The flushes*

The fresh-water flushes which occur on the plateaux are frequently dominated by *Philonotis fontana*. The water is weakly alkaline, a pH 7.4 being found. The *Philonotis* may be raised above the general water-level forming a drier mound on which the following mixture of grassland species was recorded:

<i>Agrostis vulgaris</i>	o.	<i>Hypnum schreberi</i>	f.
<i>Carex panicea</i>	o.	<i>Polytrichum commune</i>	f.
<i>Cerastium vulgatum</i>	o.	<i>Prunella vulgaris</i>	o.
<i>Festuca ovina</i>	o.	<i>Trifolium repens</i>	f.

In the wetter marginal regions *Hypnum cuspidatum* is abundant, and may be locally dominant in some examples, while on the drier outskirts the species listed below are usually present.

<i>Cardamine pratensis</i>		<i>Carex vulgaris</i>	
<i>Carex echinata</i>		<i>Juncus bulbosus</i>	
<i>C. oederi</i>		<i>J. communis</i>	
<i>C. pulicaris</i>		<i>Ranunculus flammula</i>	

One flush was found in which *Brachythecium rivulare* was dominant, the pH was 7.0 and it was associated with the undermentioned species:

<i>Callitriche stagnalis</i>	l.f.	<i>Montia fontana</i>	o.
<i>Carex echinata</i>	o.	<i>Stellaria uliginosa</i>	l.f.
<i>Hypnum cuspidatum</i>	f.	<i>Trifolium repens</i>	l.f.
<i>Juncus bulbosus</i>	l.f.		

Where the flush water spreads out over the surrounding moorland and conditions are stagnant, *Sphagnum* spp. become dominant, the pH changes to 4-4.5, and the usual *Sphagnum* bog plants are found.

*(b) The water courses*

The particular vegetation following the course of the few small streams that occur naturally varies with the locality through which they pass. On the plateaux the streams may start as outlets from the boggy hollows and support similar vegetation to the drains and areas of standing water already mentioned. They frequently cut a channel 12–18 in. (30–45 cm.) deep in which are found, in addition to the above, *Utricularia minor*, *Chara delicatula*.

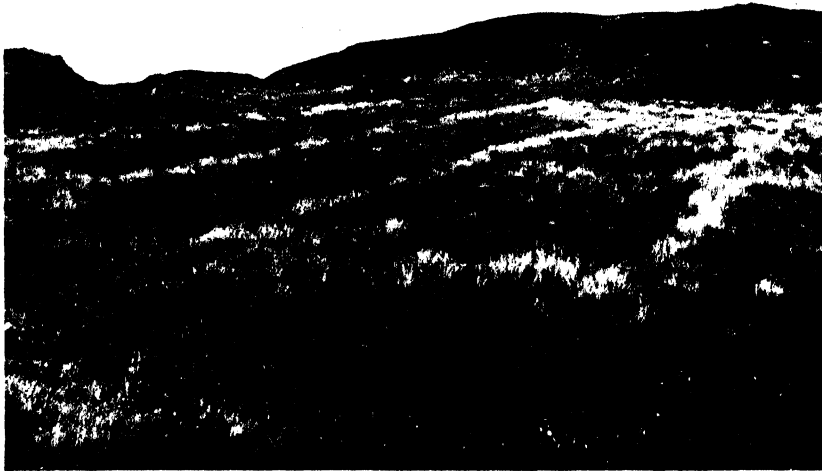
Where the streams make their way down the slopes to the coast a greater variety of plants is encountered. *Fontinalis antipyretica* is common in the water as well as *Callitriche intermedia* and *Nasturtium officinale*, whilst along the stream sides many hydrophilous species could be found. Flooding occurs where the streams pass over flat areas with consequent deposition of silt and mineral matter, here *Juncus communis* and *Iris pseudacorus* are abundant with *Anagallis tenella*, *Lemna minor*, and *Hydrocotyle vulgaris* common in muddy hollows. Similar marshy areas are to be found on Sanday, and in one relatively large marsh in the south of the island near Ant Oban dominated by *Phragmites communis* the following plants were recorded:

	<i>Phragmites communis</i>	dom.	
<i>Callitriche stagnalis</i>	f.	<i>Lycopus europaeus</i>	o.
<i>Epilobium obscurum</i>	o.	<i>Myosotis caespitosus</i>	f.
<i>Galium palustre</i>	f.	<i>Oenanthe crocata</i>	o.
<i>Glyceria fluitans</i>	f.	<i>Sparganium ramosum</i>	r.
<i>G. procumbens</i>	f.	<i>Stellaria media</i>	o.
<i>Iris pseudacorus</i>	o.	<i>S. uliginosa</i>	o.
<i>Juncus communis</i>	o.		

## SUMMARY

The basic rocks of which the islands of Canna and Sanday are composed may account for the presence of species such as *Anthyllis vulneraria*, *Koeleria cristata*, *Avena pubescens*, *Daucus carota* and *Gymnadenia conopsea*, but their effect is overshadowed by the major factor of climate in which a relatively high rainfall is associated with high atmospheric humidity. In general, topography accounts for the distribution of grassland, *Calluna* heath and moorland, the latter being confined to flat poorly drained areas such as the plateaux of Canna. Grazing and burning have allowed grassland to spread at the expense of *Calluna* heath on the slopes and mounds, but these two factors may be responsible for the spread of moorland vegetation as suggested by Fraser (1933). It is impossible to deny the resemblance of the moorland to blanket bog and to the *Scirpus* climatic moor of Fraser; no great depth of peat is to be found, however, and although *Sphagnum* spp. undoubtedly play a part in its formation, in so far as they impede surface drainage and induce acid conditions, it is the short forms that are prevalent, hummock formation being only local and largely confined to boggy depressions.

The presence of woodland and shade-loving species on the north and north-east cliffs is noted and it is suggested that they may be relicts of former woodland. At present natural tree growth is confined to an occasional stunted rowan (*Sorbus aucuparia*) on the cliffs and, it appears from information gathered from the owner of the islands, to a small patch of 'sallow' at the base of the cliffs in the south-west. Neighbouring islands of Soay and Eigg support natural oaks, birches and willows (Harrison, 1939), and there would seem to be no edaphic or climatic reason why oak-birch woodland or scrub should not be



Phot. 3. *Schoenus nigricans* filling up the drains and wet hollows of a *Sphagnum* bog.



Phot. 4. A near view of a rocky knoll in the moorland showing the transition from *Calluna* heath immediately below the summit through an area dominated by *Scirpus caespitosus* to a *Sphagnum* bog, showing hummock formation in the foreground.





found on Canna and Sanday. When the islands were more thickly populated destruction of trees for fuel, especially here where there is little peat development, combined with non-regeneration due to seedling destruction by sheep, cattle and rabbits, may account for the present paucity of natural woodland.

In conclusion thanks are due to the Carnegie Trustees whose grant enabled expeditions to the islands to take place in 1938 and 1939, and to Mr J. L. Campbell, the owner, whose help and hospitality encouraged the work. The thanks of the author are also extended to the other botanists of the party, in particular Dr R. F. Jones, who gave valuable help in listing the flowering plants.

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## OBITUARY NOTICE

FREDERIC EDWARD CLEMENTS

1874—1945

The death of Frederic Clements in July 1945 removed 'by far the greatest individual creator of the modern science of vegetation', to quote the words I wrote of him some years ago. It is impossible here to review his life's work in detail—it was far too voluminous and varied—and I shall confine myself to some estimate of his most important contribution to the theory of his subject, and some impression of his personality. The man who states a general theory which leads subsequent workers along the most fruitful lines of research performs a service which is fundamental to the progress of science, in that it helps to create the permanent *structure* of science, without which the amassing of detailed knowledge, and even the most brilliant single discoveries, can have no coherent meaning. Such a theory may be overstated, it may contain flaws which make it unacceptable in its entirety; but if it also contains, as Clements's did, a general idea of the first importance on which subsequent advance can be based, its originator's name can never be forgotten.

After graduating at the University of Nebraska in 1894, Clements's years at Lincoln, from 1894 to 1907, under the inspiring influence of C. E. Bessey and in co-operation with a number of like-minded young men, were filled with intense and enthusiastic activity over a wide range of botanical subjects, among which the fungi took an important place. In 1898, in collaboration with Roscoe Pound (who was Director of the Botanical Survey of Nebraska and afterwards became Professor of Law at Harvard and America's most famous philosophical lawyer with the highest international reputation), Clements published *The Phytogeography of Nebraska*, an able work, remarkably comprehensive for its period. This was followed, in 1904, by *The Development and Structure of Vegetation*, in which the ideas that later came to maturity were foreshadowed, and in 1905 by *Research Methods in Ecology*, a stimulating book which dealt for the first time with the practical analysis of vegetation and of habitat factors by the quadrat and transect methods and the use of instruments in the field.

In 1907 Clements became Professor and Head of the Department of Botany at the University of Minnesota, and there he stayed till 1917 when he was invited to join the Carnegie Institution of Washington as Research Associate in charge of ecological research. He was very glad to leave the severe winters of Minneapolis, which put a strain on his rather delicate health, and to be able to devote himself entirely to research. He retired from the Carnegie Institution in 1941, but actively continued his work until a few weeks before his death. During all the later part of his life he worked during the summer at the Alpine Laboratory below Pike's Peak, and during the winter at the Coastal Laboratory in the beautiful climate of Santa Barbara, California.

After successive tours through the whole of the western half of the States he published in 1916 his great work, *Plant Succession: An analysis of the development of vegetation*. In this book, replete with the detailed observations of his extensive field work and full of subtle and penetrating interpretations of the phenomena of succession, together with a

very complete consideration of American and foreign contributions, he stated his famous theory of the plant formation as an organism: 'As an organism the formation arises, grows, matures and dies.' 'The climax formation is the adult organism of which all the initial and medial stages are but stages of development.'

If we choose to define organism, as Whitehead does, so as to include, for instance, the atom, the solar system, and, indeed, the universe, we may assent to the inclusion of the climax formation. For a climax formation is certainly a 'system' in relative equilibrium, both internal and external. But that is not what Clements meant. He considered a plant formation as essentially in the same category as an individual plant or animal, and the great majority of biologists are unwilling thus to extend the denotation of the word. To them a living organism means an individual plant or animal, and the nature of a plant community differs from that of an individual in so many and such fundamental respects that to include such an aggregate of different organisms under the same concept is felt to be confusing rather than helpful. Nevertheless, the plant community has certain important characters in common with the individual, and it may be usefully considered as a 'quasi-organism'. More recently, the claim has been made that the animals inhabiting a given site should be included with the plants in the concept of community, and this 'biocoenosis' or 'biotic community' has been called a 'complex organism' by Clements's school. But the plants are a 'community' in a real sense in which the whole 'biome' is not, even though an explicit recognition that we cannot fully understand the ecology of a plant community unless we include the animals as well as the plants inhabiting the site in our study is all to the good; the same applies, of course, to the inorganic factors—climatic, physiographic and edaphic—at work on the site. And this brings us to the wider concept of a 'system', in this case what may be called an 'ecosystem', which is only an organism in the sense in which the solar system or the universe are organisms, because it shows 'organization' and a considerable degree of dynamic equilibrium.

Clements's great achievement was to bring together the important work that had been and was being done on the succession of vegetation by many Americans, outstanding among whom were Cowles and his pupil Cooper, and in this country Moss, to reinforce it with his own acute and extended observations over most of the western half of the North American sub-continent, and to integrate the whole into a general system of universal scope with a very complete and appropriate terminology. In this system the effects of climate, admittedly the primary factor in determining the distribution of the great world plant formations, were given exclusive significance, while the effects of physiographic and edaphic factors were denied their due place (as it seemed to others) in the factorial complex. In the same way the water relations, again admittedly a primary factor in determining types of vegetation, were given exclusive significance, and the chemical characters of the soil almost ignored. These features of Clements's exposition were no doubt largely due to the fact that his experience lay in a region in which the zonation of the great climatic types correlated with rainfall and air humidity was unmistakably the outstanding feature of the vegetation. Ecologists living in eastern North America and in western Europe were less inclined to take so sweeping a view.

In spite of these things and of the identification of the plant formation with an organism in the ordinary sense, there is no doubt that Clements's generalization and its masterly statement have inspired ecological work in America, Britain and the British Dominions in a very high degree, and have directly stimulated many of the most fruitful subsequent

advances. There was much criticism, both in America and Europe, some of it quite undeservedly contemptuous, some reasonable, and the latter kind contributed effectively to what were regarded, in England at least, as necessary modifications and adjustments of the Clementsian system. The strength of that system lay in its philosophical sweep and completeness, founded on its author's comprehensive insight into the phenomena of vegetation, its main weakness in a certain rigidity, and a tendency to argue *a priori* from the proposition that the formation is an organism whose existence is determined solely by climate, and that all other plant communities, whatever their degree of individuality and permanence, must be interpreted in terms of the climatic climax or formation. There was a feeling that a more empirical method, a building up of theory piece by piece, as knowledge of different kinds of vegetation and of the habitat factors increased, was more likely to lead to a sound theoretical structure.

In later years Clements recognized that climaxes other than the climatic did exist, and accordingly introduced such terms as proclimax, dysclimax, etc.; these concepts certainly brought needed supplements to the original scheme. Two of his most important later papers were published in this *Journal*—'The Relict Method in Dynamic Ecology' (1934) and 'The Nature and Structure of the Climax' (1936)—and these are well worth reading by all plant ecologists, for they contain masterly expositions of his perfected system.

During his long period of work with the Carnegie Institution Clements published a number of works on ecological and related topics, many of them in collaboration. In several of these his strong views on methods of evolution and the origin of species found expression. Like many botanists before him Clements was a Lamareckian, and he never seemed to give proper weight to the results of modern genetical research. This attitude put him rather out of touch with most of the recent work on the origin of the smaller taxonomic units, and although he carried out much transplant work between different climates, not all of his conclusions were convincing.

Though out of accord with many American botanists, Clements had, throughout his career, a devoted following of younger men, and besides exercising a world-wide influence through his theory of vegetation, he directly inspired a great deal of American ecological research. This was partly due to his powerful personality. He was decidedly puritan, even ascetic (he neither drank nor smoked, and it gave him real pain to see other people doing so), and his manner was apt to be tinged with a certain arrogance. These things naturally antagonized many people; but at the same time his capacity for continuous hard work, his intense and complete devotion to his subject, his powerful intellect and unrelenting search for fresh knowledge and satisfactory formulations, could not fail to inspire the highest respect. He was essentially reasonable in argument, and he had that best of all senses of humour which enables a man to laugh at himself. He was most kindly and considerate in all personal relationships and a thoroughly good and loyal friend, as the writer has every reason to know from the experience of more than thirty years.

A. G. TANSLEY

## R E V I E W S

**Steers, J. A.** *The Coastline of England and Wales*. Pp. 644, 2 coloured plates, 115 photographs, 114 maps and plans. 42s. net. Cambridge University Press.

The varied coastline of Southern Britain offers a surprisingly large range of interests to the naturalist and physiographer and therefore has always proved to be a source of study to the ecologist. The play of erosion and of deposition upon the plant and animal communities can be seen in a score of localities and upon varying scales—while there is often an historical background sufficient to make reconstruction of successional evidence possible.

While the present book is written primarily from the point of view of the geographer, it does for the first time give an integrated account of the coastline of England and Wales as a whole, and if only on that account it must for long remain essential to any further inquiry into the subject. It is opportune at the present moment not only because the impact of regional planning upon the coastal regions has become probable but also because in the scientific sense, an integration of existing sources of information has long been overdue. The present work is authoritative from both points of view—since its author has had the opportunity of examining and reporting on the whole of the coastline to the Ministry of Town and Country Planning—while his long-continued researches on the Norfolk coast have formed an admirable basis for the wider scientific survey.

In form, the book deals first with the basic general considerations of the geology, stratigraphical and physiographical, of England and Wales, before going on to consider in detail the various sections of the coastline—a task which occupies the greater part of the book. In the sections concerning which the reviewer has detailed knowledge, the treatment given seems to be both well-balanced and informative, and at the same time suggestive where further work is needed. The areas, for which extensive information exists as to change of status (such as the Fenslands), naturally receive a somewhat fuller treatment and general topics are thus introduced in the course of the detailed survey. This leads up to the discussion of the recent vertical movements of the shoreline. The last chapters deal with coastal dunes and salt marshes, and with their vegetation. These are especially useful as summaries of the physiographic factors involved in these plant habitats. The book is concluded by an admirable series of 115 photographs selected to show the points of especial interest and the typical features of almost the whole of the coastline. This is not the least valuable feature of a well-designed book. As a whole, it is one which must long remain the authoritative treatment of the subject. It is a work which is essential to all those interested in tidal lands.

W. H. P.

**Small, J.** *pH and Plants*. Pp. 216, 16 text-figures. 1946. 12s. net. London: Baillière, Tindall and Cox.

Twenty-six years have elapsed since W. Mansfield Clark published his book on the *Determination of Hydrogen Ions*, an event that marked the recognition of pH measurement as a biological technique and that let loose a great flood of biological literature on the effects of hydrogen-ion concentration. The diversity of this literature, and possibly also the necessity of carefully sifting from it the few grains of wheat among a large amount of chaff, seems to have deterred authors from attempting either its general analysis or a greater degree of integration. Thus Prof. Small has rendered us a considerable service in reviewing and summarizing in a small volume, the extensive botanical literature on this subject. The treatment is now considerably wider than that contained in his former *Protoplasma* monograph (*Hydrogen-ion Concentration in Plant Cells and Tissues*, 1929). In the first three chapters, he dismisses the pH scale and methods of measurement, buffers and carbon dioxide effects. Then follow chapters dealing with the relations of pH and plant sap, the cell walls, the protoplast and enzyme action. Of particular ecological bearing are succeeding chapters on pH and aquatic life (which includes also many references to animals)

and on soil pH and plants. There are concluding chapters on pH and plant pathology and pH in succulents. Appendices are added on the relation between pH and hydrogen-ion concentration and on dissociation of acids. A list of selected references for further reading is given also. Attention should here be drawn to the full treatments given to buffer effects in plant tissues and to the role of pH in stomatal action. There are characteristic touches of interest in the treatment of pectin and gelatine in relation to jam-making.

It is easy to criticize any book of this type which attempts to summarize in small space a very large body of work. In this place perhaps some reference to the chapters dealing with ecological relations is desirable and perhaps the principal thing which may be said about these chapters is to refer to the danger of attempting to generalize too widely from results obtained under different climatic and edaphic conditions. I should have thought that it would have been a bold man who would have compared results from the warmer parts of North America with those from Sweden. Thus in the lists of acidiphilous plants, it is rather surprising to see *Eriophorum vaginatum* associated with *Carex aquatilis* and it may be doubted whether species such as *Parnassia palustris*, *Thymus chamaedrys* and *Heracleum sphondylium* are entirely confined to soils of above pH 7.5. There can, however, be no question that in bringing together the material, the author has put ecologists under a distinct obligation, and that his work, consequently, will be generally appreciated.

W. H. P.

**Stiles, W.** *Trace Elements in Plants and Animals*. Pp. 189, 12 figures (photographic). 12s. 6d. Cambridge University Press.

One of the many subjects in which rapid advances have been made in recent years is the part played by traces of certain mineral elements in the nutrition of plants and animals. It can hardly be said that our knowledge has as yet advanced to the stage at which it can readily be applied to ecological problems, though curiously enough the ecological importance of the presence or absence of small quantities of certain ions, e.g. molybdenum, copper, on animal nutrition has become more clearly recognized than that of any corresponding effects of plant distribution. There are, however, already indications that one of the ways in which lime status or acidity of a soil may affect plants is in its action on the availability of metals required in small amounts. Moreover, features which we can recognize more easily in larger plants must also be those affecting soil micro-organisms and of particular interest in this respect are the relations between iron, manganese and oxidation-reduction phenomena alike in plants, in cultures and in soil.

This book is therefore timely, and Prof. Stiles has performed a valuable service in reviewing the present position in a concise and accessible form. The material is presented in four sections. The first of these is an historical introduction to the subject and it is followed by an outline of the methods used in investigating micro-nutrient problems. These include the purification of the materials used, the estimation of micro-nutrient elements in plant material and the diagnosis of mineral deficiencies in plants. The third part deals with the trace element deficiencies and with diseases of plants with particular reference to the effects of scarcity of manganese, zinc, boron, copper and molybdenum. The last section deals with the effects of trace elements in animals, particularly those of iodine, manganese, copper, zinc and cobalt. Some account is given of the function of these elements in the living organisms.

W. H. P.

**Pringsheim, E. G.** *Pure Cultures of Algae*. Pp. 119, 1 plate, 8 text-figures. 7s. 6d. Cambridge University Press.

It has been apparent for some time that considerable advances in certain ecological and hydrobiological problems were possible if the appropriate organisms could be obtained in culture. This little book summarizes the methods which may be employed in isolating and obtaining pure cultures of algae. It summarizes a great deal of Prof. Pringsheim's experience as to choice of material, suitable media and methods of the treatment and suggests ways of utilization of cultures in the laboratory. It should be particularly useful to the algal ecologist because it contains also an account of his soil and water-culture method which seems to offer unlimited possibilities for those interested in ecological problems. There is a good summary of special conditions required by certain characteristic groups and also a very serviceable list of additional references.

W. H. P.

**Whyte, R. O.** *Crop Production and Environment*. Pp. 334, plates 32, figures 53. 25s. net.  
London: Faber and Faber.

This book is an attempt to bring together the physiological and horticultural data dealing with growth and reproduction. As almost all of this work of recent years has had an economic background, it is inevitable that a book of this type should have a very strong practical bias. Indeed, the author expressly says he has attempted to bring together the material of the practical grower and to harmonize it with that of the physiologist.

The argument starts from the need to distinguish between the quantitative and qualitative aspects of growth, and accepts the current terminology which calls the former growth and the latter development. It then deals first with the morphological features, particularly those of developing growing points and with especial reference to flowering. Development (mainly of flowering) is then considered in relation to temperature, seed dormancy and 'vernalization', light and darkness. There are also chapters on hormones and reproduction and on photoperiodism, on adverse environments, and on breeding in relation to environmental requirements. Finally, there are four chapters dealing with the development and physiology of crop plants and one on tropical and subtropical crops. A useful bibliography completes the book, which is excellently illustrated.

This is essentially a reference book, but it is one which seems to include all the more important principles which have been published as well as a great wealth of illustrative examples and as a summary of existing work it will be valuable both to physiologists and ecologists.

W. H. P.



## PAPERS OF ECOLOGICAL INTEREST RECEIVED

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- Jessup, R. W.** The ecology of area adjacent to lakes Alexandrina and Albert. *Trans. Roy. Soc. S. Aust.* **70**, 3, 1946.
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- Krauss, R. W. & Kent, G. N.** Analyses and correlation of four New Hampshire bogs. *Ohio J. Sci.* **44**, 11, 1944.
- Ludi, W.** Pollenstatistische Untersuchungen interglazialer gebänderten Mergel an der Rhone unterhalb Genf. *Ber. geobot. Forschungsinst. Rübel Zürich*, **88**, 1945.
- Ludi, W.** Die Hochwasserkatastrophe im west schweizerischen Seeland vom November-Dezember, 1944. *Ber. geobot. Forschungsinst. Rübel Zürich*, **108**, 1945.
- Misra, R.** The soil complex as studied in plant ecology. *Presidential Address to Indian Ecol. Soc. Benares*, 1944.
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## THE BIOLOGICAL FLORA OF THE BRITISH ISLES

### NOTICE TO CONTRIBUTORS

The Biological Flora has now been in course of publication for five years and during this time accounts of nineteen species have been published, while accounts of over 100 other species are in various stages of preparation. With the ending of the war and the gradual return to normal conditions, the Editors expect an increase in the rate at which completed accounts are received for publication, but it is evident that if the whole British flora (about 1900 species, excluding *Rubus* and *Hieracium*, according to the recently published *Check List*) is to be dealt with in a reasonable number of years, steps will have to be taken to quicken the rate of preparation and publication of accounts. Also, in view of the great amount of printing space which will be occupied if the rate of publication is increased, steps will have to be taken to limit the length of individual accounts. The Editors would welcome any suggestions likely to promote these ends and meanwhile they make the following proposals:

1. In future accounts should not in general exceed 4000 words of text, including tables (6 pages of the *Journal*), with a further allowance of 2 pages for maps, drawings and diagrams. For a limited number of species, at the Editors' discretion, the space allowance may be increased to a maximum of 12 pages of text and 4 of diagrams, etc. Before preparing their MSS. contributors should ascertain from the Editors in which category the species they are concerned with belong.

2. The lists of species under the heading 'Communities' should be drastically curtailed. In general these data should be given in tabular form and should refer to areas of stated extent. For the smaller herbaceous associates, e.g. in woodland ground flora and grassland communities, it will usually suffice to provide lists showing the percentage occurrence ('frequency') in a stated number of metre quadrats which include the species in question.

3. A revised edition of the *Schedule for Contributors* is printed below.

Contributors to the flora are reminded that Addenda and Corrigenda to the accounts already published will be issued as soon as a sufficient number of them have been received. The Editors would be glad to be informed of any such corrections and additions.

The Editors would be glad to receive photographs of first-rate technical quality of British species including those of which accounts have already been published, growing in their natural habitats. It is proposed to issue these photographs from time to time as supplements to the flora.

**BRITISH ECOLOGICAL SOCIETY**  
**BIOLOGICAL FLORA OF THE BRITISH ISLES**  
**REVISED SCHEDULE FOR CONTRIBUTORS**

The Roman figures, *italic* letters and *italicized* titles given in this Schedule should also appear as section headings in the published accounts. Sections may consist of one or more paragraphs according to the amount of relevant information available. Where there is no information on any point specifically mentioned in the Schedule, the fact should be stated.

Accounts should in general *not exceed 4000 words of text, including tables (6 pages of the Journal) with a further allowance of 2 pages for maps, drawings and diagrams*. For a limited number of species, at the Editors' discretion, the space allowance may be increased to a maximum of 12 pages of text and 4 of diagrams, etc.; before preparing their MSS. contributors should ascertain from the Editors in which category the species they are concerned with belong. For British vascular plants nomenclature should follow the 'Check-list of British vascular plants' (*J. Ecol.* **33**, 1946, pp. 308-47). For bryophytes referred to in the text nomenclature should follow the *Census Catalogue of British Mosses* (2nd ed. 1926) and the *Census Catalogue of British Hepatics* (3rd ed. 1930). 'Authorities' for names of British plants other than fungi need not be quoted, but should be given for fungi and all non-British plants and for the names of animals. References should follow the memorandum on 'References in the Biological Flora' (*J. Ecol.* **32**, 1944, pp. 116-17). On the map the types of shading desired, and the limits of the distribution in the inset map of Europe should be marked *in pencil*; suitable mechanical tints will be applied by the printers.

### SCHEDULE

**NAME.** (The name of the species should be followed by the number according to the *London Catalogue of British Plants* (11th ed. 1925), and if necessary by not more than one or two of the most important synonyms.)

**TAXONOMIC DESCRIPTION.** Subgenus or section to which species belongs. Variability, including mention of subspecies, varieties, ecotypes, forms, etc., known to be British (see 'Memorandum on Nomenclature and Taxonomy in the Biological Flora, *J. Ecol.* **31**, 1943, pp. 93-6). A brief statement of the status (native, naturalized, etc.) of the species, and of its habitat or habitats.

**I. Geographical and altitudinal distribution.** Distribution\* and abundance in the British Isles. Extra-British distribution. Altitudinal limits in Britain and abroad.

**II. Habitat.** (a) *Climatic and topographical limitations.* Climatic (including micro-climatic) limitations and preferences with regard to temperature, rainfall, atmospheric humidity, exposure to wind, etc. Light intensity and its seasonal variation in relation to the life history and distribution of the species. Topographical limitations and preferences

\* Contributors who wish to consult the most recent vice-comital records should send their data of vice comital distribution (with a stamped and addressed envelope) to Mr A. J. Wilmott, 17 Melrose Road, Merto Park, London, S.W. 19, asking him to check them against his annotated copy of Druce's *Comital Flora*.

(restriction to north- or south-facing slopes, open or shaded habitats, etc.). Tidal range, etc., for maritime species.

(b) *Substratum*. Parent material. Appearance of soil profile. Height and seasonal variation of the water table. Abundance of worms and other burrowing animals. Rate of decay and incorporation of humus. Appearance and texture of raw humus or peat, if present. pH at different depths, stating how determined: the depths should be selected in relation to the layers of the soil profile and the rooting depth of the characteristic plants. Humus content or 'loss on ignition'. CaCO<sub>3</sub> content. Other chemical analyses (potassium, phosphate, total nitrogen, nitrate nitrogen, salinity, etc.). Mechanical analyses.

Where a species occupies a great variety of habitats it may be impossible to give precise information under all the above headings, but some indication of ranges and of the characteristics of the most frequent habitats will be valuable.

III. *Communities*. Communities in which the species occurs with its frequency in each and with lists of closely associated species.

Complete lists with frequency symbols should be given if possible, but lists only of the chief associated species, and especially of the dominants, will be adequate. The most useful form in which to give this information is a table with the names of associated species in the left-hand column, the remaining columns showing the frequencies in the various localities named at the heads of the columns. These frequencies may be indicated by the conventional symbols or by figures representing the percentage occurrence of the associated species in a stated number of quadrats (e.g. of 1 sq.m. for herbaceous plants), all of which include the species in question. It is important that any one list should refer only to one kind of habitat and to restricted areas including the species in question. Lists should include characteristic species of other groups than Flowering Plants, if possible.

IV. *Response to biotic factors*. Effect of felling, burning, coppicing, mowing, peat-cutting, grazing, rabbit-nibbling, trampling, manuring, ploughing, etc.

V. (a) *Gregariousness*. Solitary plants, large patches, small patches, etc.

(b) *Performance in various habitats*. Average height; whether flowering freely, poorly, not at all; whether setting seed, etc.

(c) *Effect of frost, drought, etc.* Sensitivity to exceptional weather conditions.

VI. (a) *Morphology*. Form, depth, direction of growth and length of underground stems and functional roots. Other morphological data only if of special ecological importance.

(b) *Mycorrhiza*. Presence or absence of mycorrhiza and its type if present.

(c) *Perennation; reproduction*. Raunkiaer life-form. Mode of perennation and general description of winter conditions. Mode and rate of vegetative reproduction and spread. Longevity of the individual plant. Age of plant at first flowering. Does the plant set seed (or produce seedlings) every year, or at what interval?

(d) *Chromosome number*. State the authority and the source (British or foreign) of the material examined.

(e) *Physiological data*. Transpiration rates, osmotic values, etc, when relevant.

VII. *Phenology*. Times of maximal growth of roots and other underground organs; of appearance of new leafy shoots; of flowering; of maturation and shedding of seeds; of germination of seeds.

VIII. (a) *Floral biology*. Mode of pollination of flowers. Insect visitors to flowers and their behaviour. Are the flowers self-compatible? Are cleistogamic flowers produced, and, if so, when? Is reproduction amphi- or apomictic? Does vivipary occur?

(b) *Hybrids*. Existence and frequency of natural hybrids. By what criteria are the hybrids recognized as such? To what extent do the hybrids show a diminished fertility as compared with the parents? Do they show any differences in ecological behaviour?

(c) *Seed production and dispersal*. Average numbers of seeds per fruit and per plant. Mode of seed dispersal and special features, if any, e.g. seeds tend to stick together.

(d) *Viability of seeds; germination*. Viability of seeds under different conditions (state how determined). Place of germination under natural conditions. Special conditions affecting germination, e.g. sensitivity to light, necessity for preliminary freezing, etc. Conditions for successful establishment of seedlings.

(e) *Seedling morphology*. Short description and sketch of young seedlings.

(f) *Effective reproduction*. Relative importance of reproduction by seed and by vegetative means.

IX. (a) *Animal feeders or parasites*. Insects or other animals feeding on the plant, and the part or parts eaten by them.

(b) *Plant parasites*. Fungi or other plants of which the species is a host, and the parts attacked by them.

(c) *Diseases*. Descriptions of the symptoms and the names of causal organisms, if any, of diseases causing serious damage. Assess as far as possible the importance of the damage done by the diseases. Does the incidence of the disease vary with habitat and season?

Contributors should, as early as possible, send provisional lists of insects and fungi, with stamped and addressed envelopes, to Dr O. W. Richards (Imperial College Field Station, London Road, Slough, Bucks) and Dr Alex. Smith (Plant Pathological Laboratory, Ministry of Agriculture and Fisheries, Milton Road, Harpenden, Herts) respectively, who have kindly consented to assist contributors with references to these groups.

#### NOTE ON REFERENCES TO INSECTS (O. W. RICHARDS)

The lists of insects will in general be restricted to those closely associated with a single genus or species of plant, but may include some which feed on two or more allied genera of plants, or on a few genera living in the same habitat. Insects for which the records do not state the individual species of plants will be listed only in the accounts of genera.

Sometimes insects with polyphagous feeding habits may actually be more common on a plant than the restricted feeders, but the list of general feeders would be extremely long and very difficult to make complete. Where a general feeder is actually known to be a serious check to a plant, the record will be included.

Only British insects will be listed, but they will include some whose feeding habits may have been observed only on the Continent. Records will be given of the British distribution, in a very condensed form, where there is reason to think the information reliable. Absence of records often means that an insect has not been collected rather than that it is not present. The very imperfect state of the records of insect feeding habits and distribution must be stressed.

Lists will be given of the larger works from which the records have been taken, and of the experts who have been consulted.

X. *History*. A brief account of the history of the species as a member of the British flora, with notes on fossil records, dates of introduction of denizens and aliens, etc.

# **BIOLOGICAL FLORA OF THE BRITISH ISLES**

## ACCOUNTS PUBLISHED OR IN PREPARATION

The parts already published are:

- Juncus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. inflexus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. effusus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. conglomeratus* L., by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- J. subnodulosus* Schrank, by P. W. Richards and A. R. Clapham. *J. Ecol.* **29**, no. 2.
- \**Zostera* L., *Z. marina* L. and *Z. hornemanniana* Tutin, by T. G. Tutin. *J. Ecol.* **30**, no. 1.
- Cladium mariscus* R.Br., by V. M. Conway. *J. Ecol.* **30**, no. 1.
- Aster tripolium* L., by A. R. Clapham, W. H. Pearsall and P. W. Richards. *J. Ecol.* **30**, no. 2.
- Juncus filiformis* L., by P. W. Richards. *J. Ecol.* **31**, no. 1.
- J. macer* Gray, by P. W. Richards. *J. Ecol.* **31**, no. 1.
- \**Rhamnus cathartica* L. and *Frangula alnus* Mill, by H. Godwin. *J. Ecol.* **31**, no. 1.
- Tamus communis* L., by I. H. Burkill. *J. Ecol.* **32**, no. 1.
- Acer campestre* L. and *A. pseudo-platanus* L., with a note on *A. platanoides* L., by E. W. Jones. *J. Ecol.* **32**, no. 2.
- \**Polygonum* L. em Gaertn., *P. persicaria* L., *P. lapathifolium* L. and *P. petecticale* (Stokes) Druce, by N. W. Simmonds. *J. Ecol.* **33**, no. 1.
- Gentiana pneumonanthe* L., by N. W. Simmonds. *J. Ecol.* **33**, no. 2.
- Allium vineale* L., by Mrs Ruth H. Richens.

These may be obtained from the Cambridge University Press, 200 Euston Road, N.W. 1, at 1s. each; those marked with an asterisk are sold as double parts, 2s. Standing orders for all parts issued may be placed at the reduced price of 9d. each, double parts 1s. 6d.

The following are being prepared:

- Aconitum anglicum* Stapf, H. A. Hyde, National Museum of Wales, Cardiff.
- Adoxa moschatellina* L., Prof. M. Skene, The University, Bristol.
- Alchemilla vulgaris* agg., *A. alpina* L., and *A. conjuncta* Bab., S. M. H. Walters, The Botany School, Cambridge.
- Allium ursinum* L., T. G. Tutin, University College, Leicester.
- Anagallis arvensis* L. and *A. foemina* Mill., J. L. Crosby, Department of Botany, The University, Durham.
- Andromeda polifolia* L., Prof. W. H. Pearsall, F.R.S., Department of Botany, University College, Gower Street, W.C. 1.
- Anemone nemorosa* L., A. C. Crundwell, Loadhams, Farnham, Surrey.
- Arenaria verna* L., Dr K. Blackburn, King's College, Newcastle-on Tyne.
- A. norvegica* Gunn., Dr W. A. Clark, King's College, Newcastle-on-Tyne.
- Arum maculatum* L., F. A. Sowter, 9 North Avenue, Leicester.
- Asperula odorata* L., Prof. A. R. Clapham, Department of Botany, The University, Sheffield.

- Atropa belladonna* L., Dr R. W. Butcher and Dr W. O. James, University Department of Botany, Oxford.
- Blackstonia perfoliata* (L.) Huds., Dr B. Colson, University Department of Botany, Reading.
- Carex acutiformis* Ehrh., *C. bigelowii* Torr., *C. curta* Good., *C. disticha* Huds., *C. riparia* Curt., and *C. saxatilis* L., E. Vernon Watson, University Department of Botany, Reading.
- Carex flacca* Schreb., F. J. Taylor, University College, Leicester.
- Carlina vulgaris* L., *Cirsium palustre* (L.) Scop. and *C. vulgare* (Savi) Airy-Shaw (*C. lanceolatum* (L.) Scop.), Dr W. A. Sledge, University Department of Botany, Leeds, 2.
- Clematis vitalba* L., O. Polunin, Charterhouse, Godalming.
- Colchicum autumnale* L., Dr R. W. Butcher, Culford House, Ewe Lamb Lane, Bramcote, Notts.
- Corallorrhiza trifida* Châtel., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.
- Cornus sanguinea* L., J. W. Wilson, Department of Botany, Oxford.
- Cuscuta europaea* L., Bernard Verdcourt, 86 Claremont Road, Luton, Beds.
- Danaa cornubiensis* (L.) Burnat, Dr G. Pethybridge, Penlee, Harleigh Road, Bodmin.
- Daphne laureola* L., Dr P. W. Richards, The Botany School, Cambridge.
- Elymus arenarius* L., T. E. T. Bond, Tea Research Institute, Ceylon.
- Epilobium nummularifolium* R.Cunn., Miss A. J. Davey, Department of Botany, Memorial Buildings, Bangor.
- Eriocaulon septangulare* With., Dr Leighton Hare, Jodrell Laboratory, Royal Botanic Gardens, Kew.
- Galium debile* Desv., *G. palustre* L. and *G. uliginosum* L., A. C. Crundwell, University Department of Botany, Oxford.
- G. erectum* Huds. and *G. mollugo* L., Miss M. Priestley, c/o The Botany School, Cambridge.
- Glaux maritima* L., Miss C. M. Gibson, Municipal College, Portsmouth.
- Glyceria declinata* Bréb., *G. plicata* Fr. and *G. fluitans* (L.) R.Br., Miss J. M. Lambert, Westfield College, Hampstead, N.W. 3.
- G. maxima* (Hartm.) Holmb., Miss J. M. Lambert, Westfield College, Hampstead, N.W. 3.
- Goodyera repens* R.Br., Prof. J. R. Matthews and Dr Downie, University Department of Botany, Old Aberdeen.
- Helictotrichon (Avena) pratense* (L.) Pilger and *H. pubescens* (Huds.) Pilger, Dr G. Carson, School of Agriculture, Cambridge.
- Juncus articulatus* L., em. Wahlenb. and *J. acutiflorus* Ehrh. ex Hoffm., Prof. A. R. Clapham, Department of Botany, The University, Sheffield.
- J. squarrosus* L., Prof. W. H. Pearsall, F.R.S., University College, Gower Street, London, W.C. 1.
- J. triglumis* L., Dr W. A. Clark, King's College, Newcastle-on-Tyne.
- Juniperus communis* L., T. G. Tutin, University College, Leicester.
- Leontodon leysseri* (Wallr.) Beck (*Thrincia hirta* Roth) and *L. hispidus* L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.
- Leucojum aestivum* L., Dr F. B. Hora, University Department of Botany, Reading.
- Limosella aquatica* L., Dr F. W. Jane and Miss R. Dowling, Department of Botany, University College, Gower Street, London, W.C. 1.

- L. subulata* Ives, Dr K. Blackburn, King's College, Newcastle-on-Tyne.
- Listera cordata* (L.) R.Br., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.
- Lloydia serotina* (L.) Reichb. and *Lobelia dortmanna* L., Dr N. Woodhead, University Department of Botany, Bangor, North Wales.
- Luzula forsteri* (Sm.) DC. and *L. pilosa* (L.) Willd., Prof. T. Harris, University Department of Botany, Reading.
- L. sylvatica* (Huds.) Gaud., Miss E. M. Leyland, 25 Devon Street, Barrow-in-Furness, Lancs.
- Melandrium dioicum* (L.) Coss. & Germ. and *M. album* (Mill.) Garcke, H. G. Baker, University Department of Botany, Leeds, 2.
- Myosotis arvensis* (L.) Hill, *M. collina* Hoffm. and *M. versicolor* Sm., A. E. Wade, National Museum of Wales, Cardiff.
- Myrica gale* L., Miss A. J. Davey, Dept. of Botany, Memorial Buildings, Bangor.
- Naias flexilis* Rostkov, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
- Narcissus pseudo-narcissus* L., Dr J. Caldwell, University College, Exeter.
- Nardus stricta* L., R. Elfyn Hughes, Department of Agricultural Botany, Bangor.
- Narthecium ossifragum* (L.) Huds., Dr Mollison, University Department of Botany, Old Aberdeen.
- Nasturtium officinale* R.Br., H. W. Howard, School of Agriculture, Cambridge.
- Obione portulacoides* (L.) Moq., and *O. pedunculata* (L.) Moq., Prof. V. J. Chapman, c/o The Botany School, Cambridge.
- Ophrys arachnites* Hoffn., Francis Rose, The Forge House, East Malling, Kent.
- Orchis fuchsii* Druce, *O. elodes* Gris., *O. latifolia* L. sec. Pugsl. (*O. incarnata* auct. angl.) and *O. purpurella* Stephenson, Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
- O. purpurea* Huds., Francis Rose, The Forge House, East Malling, Kent.
- Oxalis acetosella* L., Miss Ethel Bolton, King's College, Newcastle-on-Tyne.
- Potamogeton coloratus* Hornem., *P. filiformis* Pers. and *P. pectinatus* L., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
- P. gramineus* L. and *P. rutilus* Wolfg., Dr W. A. Clark, King's College, Newcastle-on-Tyne.
- Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl., Dr E. W. Jones, Imperial Institute of Forestry, Oxford.
- Ranunculus aquatilis* agg., Dr R. W. Butcher, Culford House, Ewe Lamb Lane, Bramcote, Notts.
- Rhynchospora alba* (L.) Vahl and *R. fusca* (L.) Ait. f., Miss E. Canton, Department of Biology, Technical College, Sunderland.
- Rosa* spp. (excl. *R. arvensis*, *micrantha* and *tomentosa*), Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.
- Rumex* spp., J. E. Lousley, 7 Penistone Road, Streatham Common, S.W. 16.
- Scilla non-scripta* (L.) Hoffmanns. & Link, Prof. G. E. Blackman, Department of Rural Economy, Oxford.
- Sedum acre* L., Dr B. Barnes, Department of Biology, Chelsea Polytechnic, London, S.W. 3.



*Sinapis arvensis* L., G. E. Fogg, Department of Botany, University College, Gower Street, W.C. 1.

*Sonchus asper* (L.) Hill and *S. oleraceus* L., em. Hill, R. A. Lewin, c/o The Botany School, Cambridge.

*S. palustris* L., Francis Rose, The Forge House, East Malling, Kent.

*Spiranthes stricta* Nels., Prof. J. W. Heslop Harrison, F.R.S., King's College, Newcastle-on-Tyne.

*Stellaria nemorum* L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

*Subularia aquatica* L., Dr N. Woodhead, Department of Botany, Bangor.

*Suaeda fruticosa* (L.) Forsk., and *S. maritima* (L.) Dum., Prof. V. J. Chapman, c/o The Botany School, Cambridge.

*Thlaspi alpestre* L., Dr K. Blackburn, King's College, Newcastle-on-Tyne.

*Tilia cordata* Mill. and *T. platyphyllos* Scop., H. A. Hyde, National Museum of Wales, Cardiff.

*Triantalis europaeus* L., Prof. J. R. Matthews, University Department of Botany, Old Aberdeen.

*Ulmus* spp., Dr R. Melville, The Herbarium, Royal Botanic Gardens, Kew.

*Urtica* spp., P. Greig-Smith, Department of Botany, The University, Manchester.

*Vaccinium vitis-idaea* L., P. A. Tallentire, 14 Hulme Hall Avenue, Cheadle Hulme, Cheshire.

*Valeriana officinalis* L. and *V. sambucifolia* Mikan, J. Carpenter, Department of Botany, King's College, Strand, W.C. 2.

*Veronica anagallis-aquatica* L., *V. aquatica* Bernh. and *V. beccabunga* L., J. H. Burnett, Department of Botany, Oxford.

*Viburnum lantana* L. and *V. opulus* L., Dr H. Godwin, The Botany School, Cambridge.

*Viola lutea* Huds. and *V. tricolor* L., Dr P. E. Fothergill, King's College, Newcastle-on-Tyne.

*Wahlenbergia hederacea* Reichb., Francis Rose, The Forge House, East Malling, Kent.

The assistance of members of the Society will be greatly welcomed by the authors who are preparing these accounts. Information should be sent direct to the addresses given above. Anyone wishing to write an account singly or in collaboration should communicate with one of the members of the Committee or with the Hon. Secretary of the Society.

Accounts ready for publication should be sent to Dr P. W. Richards, The Botany School, Cambridge.

## BIOLOGICAL FLORA OF THE BRITISH ISLES

L.C. (Ed. 11) No. 1862

*Allium vineale* L.

RUTH H. RICHENS

Sect. PORRUM. Bulbous perennial, conspicuous chiefly in the season of flowering (Figs. 2 and 3), when the overground system consists of distichously arranged foliage leaves. These appear in autumn and die back in August, arising radically in succession

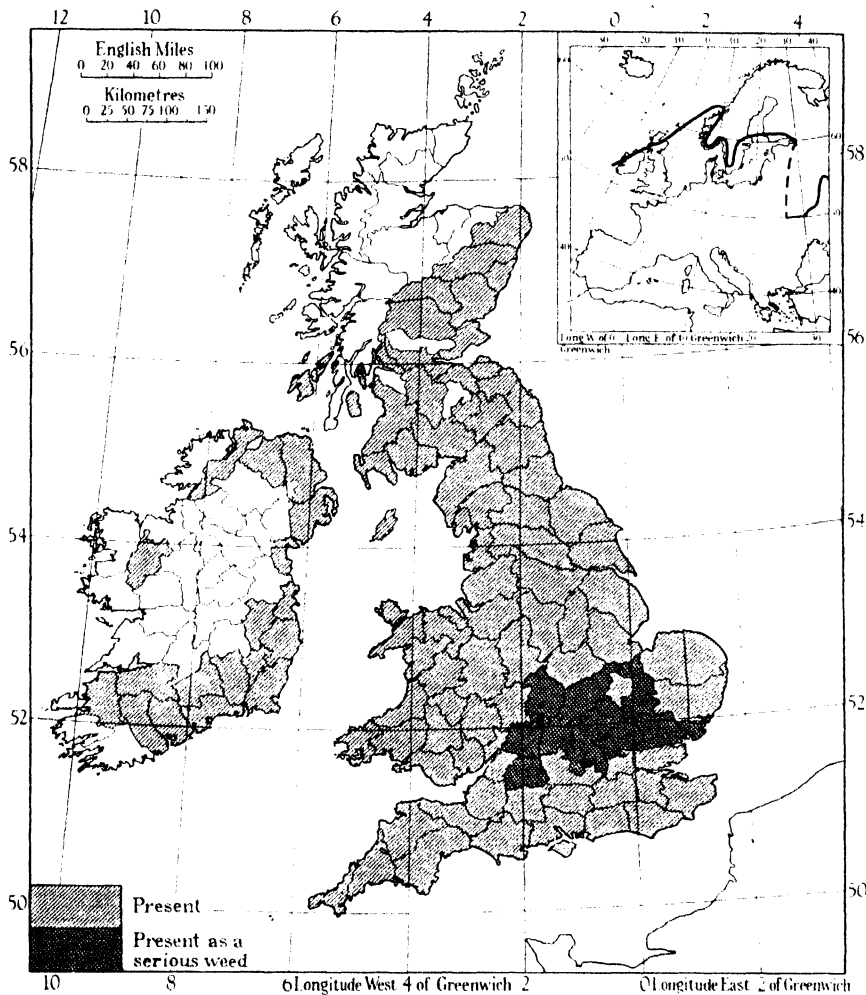


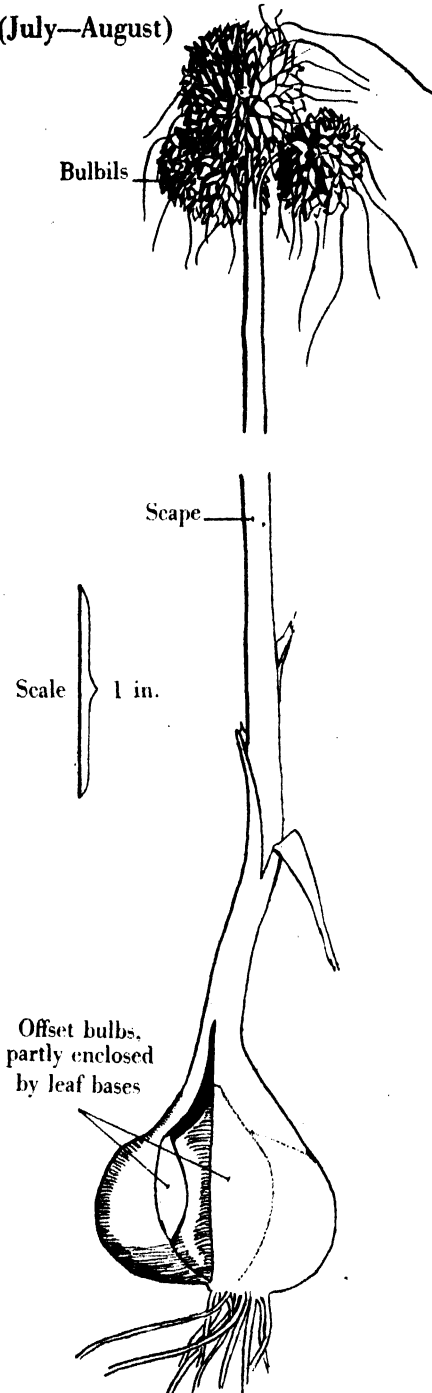
Fig. 1. *Allium vineale* L.: vice-comital distribution in the British Isles, and (inset) northern and eastern limits in Europe.

round the growing point, their bases swelling for a brief period during the growing season to the layers of the bulb. First leaf a hollow sheath only, 3–5 cm. long, elliptic in cross-section and with a sharp-pointed tip which pierces the soil surface; ensuing leaves have sheathing bases surmounted by hollow blades, slightly ribbed, crescentic in cross-section below, partially enclosing the elongating blade of the next succeeding leaf. Stem apex

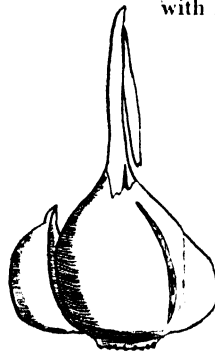
commencing to elongate in April and emerging in May from the sheath of the innermost foliage leaf as a green, terete scape; its tip enclosed in the final foliar member, a mem-

**A. Mature plant**

(July—August)



**C. Terminal bulb with lateral bulbs**



**B. Mature plant**

underground parts, leaf bases removed

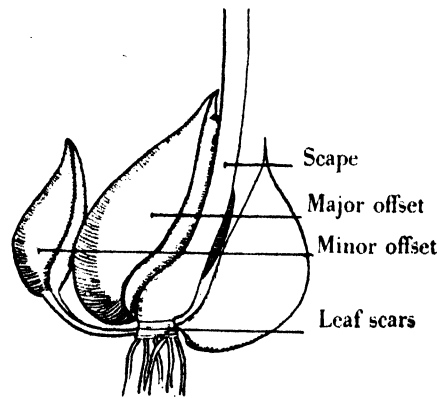


Fig. 2.

branous spathe, within which it swells to form a terminal umbel of bulbils, sometimes interspersed with flowers. Spathe usually 1-valved bursting in June, exposing a compact head, which may split into 2, 3 or 4 parts.

Lateral buds form in early spring in the foliage leaf axils, and develop into offset bulbs,

which replace the parent bulb at the end of the growing season. Rarely these are borne on long stalks (cf. *Allium sphaerocephalum*) and appear above ground in the leaf axil where the sheath splits.

Only a fraction (not more than about 30%) of any population consists of such scapigerous plants in any season; the rest is made up of smaller, less conspicuous plants, with shorter, more slender foliage during the growing season, which dies back during May or June. After the production of foliage leaves, scale leaves, usually two, develop round the growing point, the outer becoming a dry, protective covering to the inner fleshy scale of the perennating bulb. This bulb, the 'terminal' bulb, is dormant during the summer months.

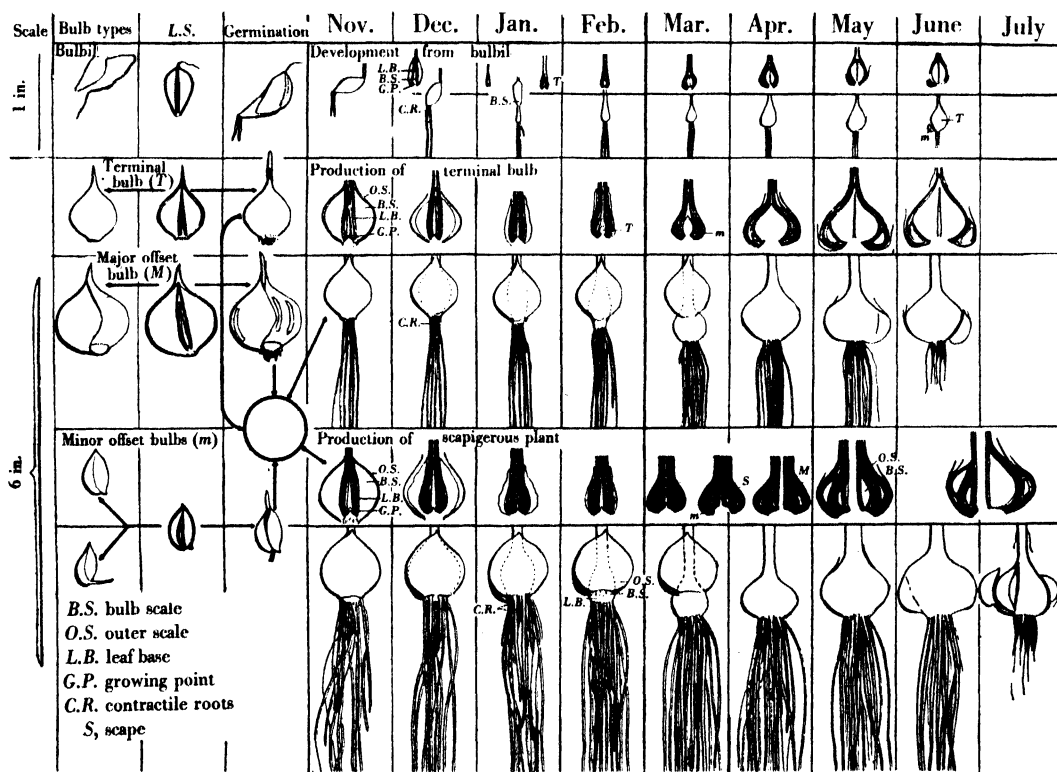
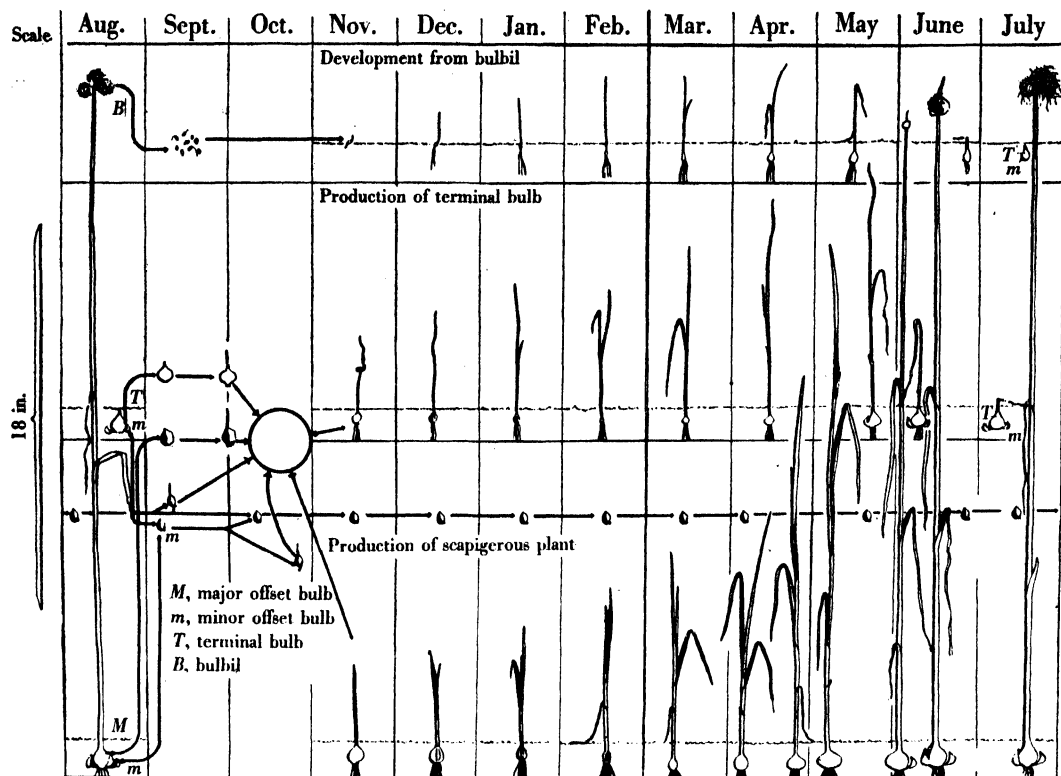
Reproduction almost entirely vegetative by means of offset bulbs and bulbils. These may take from one to several years to reach the flowering stage. Flowers, when present, pedicellate, pale rose-violet, perianth segments tinged with pink or sometimes with green along the keel, this being most marked in those of the outer whorl. Stamens exserted, filaments adnate to the perianth at the base; those of the outer whorl simple, with deep pink filaments, those of the inner whorl with pale filaments, broadened at the base, and divided about half way along their length into three points, the central one of which bears the anther. Capsule elongate, trilocular, trigonous with winged flanges; style single, central, pink, arising from a slight depression at the top of the capsule. Seeds black, triquetrous, two in each loculus (Syme, 1869), but rarely all developing.

Taxonomically the species is closest to *A. sphaerocephalum*, which is the only other British species of sect. *Porrum* possessing fistular leaves. Aerial bulbils do not occur in the latter, and other points of distinction are found in the 1-valved spathe of *A. vineale* and in the relative proportions of the stamen filaments. The spathe may, however, be 2-valved (Regel, 1875), and specimens have been seen where it appeared to have split into several irregular parts. In most of these specimens from the collection in the Welsh National Herbarium the spathe was well over 10 cm. instead of the usual 2–3 cm. (cf. *A. vineale* var. *virens* Boiss. in Rouy, *Fl.* 12, p. 350.) Statements in the literature on the proportions of the stamen filaments are at variance. The conflicting accounts may be due to the fact that the filaments elongate as the flower opens, those of the inner whorl being followed by those of the outer, and none of the records state to what stage the diagnoses given refer. One specimen has been observed in which all the stamens were apparently simple, the flowers being larger, of a clearer rose colour, and the perianth members more strongly keeled than usual.

Three varieties are commonly recognized in Britain, distinguished on the basis of the occurrence of bulbils and/or flowers on the head: (i) var. *bulbiferum* Syme with a mixture of flowers and bulbils; (ii) var. *compactum* Thuill. with bulbils only; (iii) var. *capsuliferum* Koch with flowers only. The status of these varieties is doubtful. The two former are the most frequent forms, and usually occur together; var. *capsuliferum* is rare. From observations on the occurrence of the two bulbiferous types it seems that the presence or absence of flowers in the head is purely a matter of chance, the number of flowers when present ranging from 1–2 to 20–30, and the number of bulbils being in some instances only a few.

A plant of wide distribution in Britain, found mainly as a weed of cultivation and on roadsides.

I. *Geographical and altitudinal distribution.* Recorded in Britain from all vice-counties from Aberdeen southwards, except south-west Yorkshire (63), Renfrew (76), Peebles (78),



Figs. 3, 4. Developmental cycle of *Allium vineale* in Cambridgeshire. Left-hand column of Fig. 3 illustrates mature scapigerous plant, together with the terminal bulb, in August; the possible roles of the various reproductive bodies in the life-cycle are indicated by arrows. Subsequent development is shown month by month in succeeding columns, in three horizontal series. Details of bulb structure before germination and at different stages of development are shown in Fig. 4.

and west Perth (87). Also recorded farther north from Dunbarton (99), Clyde Isles (100), and south Ebudes (102). The vars. *bulbiferum* and *compactum* are of general occurrence, but var. *capsuliferum* is only recorded from Cornwall, Wiltshire and Kent. Praeger (*Ir. Top. Bot.*) describes the species as of very local occurrence in Ireland and found chiefly in the south and east; it is recorded from vice-counties 1, 2, 4-9, 11-13, 19-21, 26, 31, 34, 38-40. Present also in Jersey and Guernsey.

Distributed throughout west and central Europe, but absent from Salzburg and north Tirol; extends northwards to the southern parts of Norway and Sweden and eastwards to southern Finland. Present in the Baltic border states excepting Estonia, and in Russia recorded from the central Dnieper region, the Crimea and east and west Transcaucasia. Apparently absent from Bulgaria and Rumania. Present in Syria. Introduced in North America.

In north Yorkshire ascending to over 1500 ft. (457 m.) (Baker, 1906). Ascends to 1700 m. in Alps of Valais (Hegi, *Fl.* 2).

II. *Habitat*. In Britain a weed of open, cultivated ground as well as of pastureland, also found in waste places and frequently on roadsides; rarely in woods. Most county records are from dry, waste places, usually sandy, and wall-tops are not infrequently mentioned as typical habitats, but in eastern England at least it is typical of heavy clay soils. In Cambridgeshire it does indeed grow on all soil types, with the exception of the fen peat, and is found in most parts of the county, particularly on road verges. But only on the gault and boulder clay soils is it an abundant weed of cultivated places. In other counties where the plant occurs as a serious agricultural weed it is also prevalent chiefly on the heavy soils. It appears that the plant can flourish over a wide range of soils but is unable to withstand cultivation on the lighter ones. The full causes of this are not known, but one important factor is probably the different types of cultivation usual to the different soil types (cf. IV).

Occurs in both cultivated and waste places throughout most of its European range, including south-east Sweden, but there is no information as to the soils on which it is prevalent as a weed on the Continent. Occurrence in Scandinavia, however, mostly in maritime districts, on sandy beaches, thickets near the shore or coastal rocks. In Denmark (Jessen, 1935, p. 101) almost exclusively a coastal plant, only rarely occurring farther inland as a field weed, but apparently unable in general to withstand cultivation. There are some records of its occurrence along the coast in certain Irish localities and from the Channel Islands, and in Britain the same is found in Sussex and South Devon. Occurs as a weed in European parts of U.S.S.R. where it is present (Vvedensky, 1935).

The following are data for a type of soil typical of that where the species occurs most abundantly as a field weed:

(a) *Parent material*. Gault clay.

(b) *Appearance of the soil profile* (Nicholson & Hanley, 1936). Horizon 1. A yellowish-grey heavy clay soil with occasional flints or pebbles. Top 5-6 in. darker in colour and in old grassland greyish-black. Horizon 2. Below (1) is bluish-grey clay with orange-coloured mottling, small and numerous markings at first, larger as the depth increases. Horizon 3. Below (2) is a characteristic horizon much the same as (2) in colour and mottling, but carrying streaks or pockets of white crystalline material. Horizon 4. Homogeneous blue-grey clay.

(c) *Water relations* (Nicholson, 1942). Soil impermeable except to the extent it is opened up by tillage, and lies wet or waterlogged except in dry seasons; moisture content fairly constant throughout the winter. Effective percolation restricted to surface layers where there is a fairly open tilth. In grassland a well-developed crumb structure at the surface gives way rapidly to soil with much less frequent cleavage planes; a marked decrease in moisture content from the surface to the 5 in. level, a less rapid decrease to 10 in., below which it varies little. On arable land there is a sudden change at the depth of tillage from an open structure to impermeable subsoil, and this gradient is not found. Hence water accumulates only in the surface layers and on agricultural land mole drains are generally used to get rid of this surplus. In summer the soil dries out from the surface, to depths as great as 80 in., and there is a marked shrinkage with desiccation, and fissuring to considerable depths; re-expansion in ensuing autumn may not completely obliterate these fissures which will thus increase the permeability of the soil for a while.

(d) *Abundance of worms, etc.* No information.

(e), (f) *Rate of incorporation and appearance of raw humus.* No information.

(g)-(k) *Mechanical and chemical analyses.* The analysis, from the Cambridge University Farm (Table 1), is typical of the gault clay in this locality.

Table 1. *Analysis of a gault soil profile, Cambridge University Farm*  
(Nicholson & Hanley, 1936, p. 35)

A.E.A. method, 1927	Horizon 1 %	Horizon 2 %	Horizon 3 %	Horizon 4 %
Coarse sand	3.9	2.9	0.02	0.03
Fine sand	7.4	6.8	0.2	0.2
Silt	17.7	17.5	11.4	12.5
Clay	61.1	61.1	51.6	52.2
Moisture	5.8	6.0	4.1	3.7
Loss on solution	1.5	1.5	1.0	0.8
CaCO <sub>3</sub>	7.9	10.1	35.1	36.2
Loss on ignition	9.9	8.1	5.3	6.1
Nitrogen	0.19	0.13	0.04	0.04
Exchangeable CaO	0.89	0.89	0.99	0.37
48 hr. HCl extract				
Insoluble residue	52.8	51.5	32.72	33.43
Fe <sub>2</sub> O <sub>3</sub>	4.32	4.80	2.96	3.08
Al <sub>2</sub> O <sub>3</sub>	15.91	16.03	14.89	14.13
CaO	5.27	6.21	20.16	20.75
MgO	0.97	0.90	1.03	0.82
K <sub>2</sub> O	1.40	1.44	1.44	1.44
P <sub>2</sub> O <sub>5</sub>	0.15	0.15	0.13	0.08
SO <sub>3</sub>	—	—	1.9	0.17

*Data for other soils.* The species occurs equally on boulder clay soils in Cambridgeshire. These are also badly drained; percolation is negligible, and waterlogging and surface pools common in wet weather. Here again, mole draining is employed on agricultural land.

In the same county, the species is noticeably absent from gravel soils except occasionally on road verges. These soils are of variable composition, but on the whole are light and well drained. The following analysis, also from the Cambridge University Farm, show the transition in soil conditions from gault to gravel, over an area similar to that from which the species lists on p. 216 are taken.

Table 2. *Soil conditions at intervals of 80 yards (73 m.), Cambridge University Farm*  
(Nicholson & Hanley, 1936, p. 68)

Geological formation ...	Gault					Old river gravel		
Type of drains ... ..	Mole drains					Occasional tiles		
Topography ... ..	Flat-depressed		Gentle slope	Moderate slope		Flat-elevated		
	1	2	3	4	5	6	7	8
Soil type ... ..	Clay on clay (%)	Clay on clay (%)	Clay loam on clay (%)	Clay loam on clay (%)	Clay loam on clay (%)	Medium loam on clay (%)	Loamy sand on clay (%)	Gravelly coarse sand on gravel (%)
<i>Top soil</i>								
Coarse sand	8	9	10	10	16	44	55	81
Fine sand	10	9	15	13	14	14	12	4
Silt	20	20	28	28	30	13	13	4
Clay	44	42	32	32	28	22	14	5
CaCO <sub>3</sub>	1.4	4.4	1.5	2.4	0.5	0.0	0.0	0.3
Altitude	40 ft.	40 ft.	45 ft.	55 ft.	65 ft.	75 ft.	75 ft.	75 ft.
Approx. depth to underlying clay	6 in.	6 in.	6 in.	6 in.	1 ft. 6 in.	1 ft. 6 in.	2 ft.	10-15 ft.
Correlation with species list on p. 216	Lower region, with abundant <i>A. vineale</i>		Middle region			Upper region, <i>A. vineale</i> rare		

III. *Communities.* Occurrences in natural communities such as shingle beaches, shore thickets and rock cliffs, where it is found typically in Scandinavia, are rare in this country. A few such records exist, but the plant is rare in such habitats and no data of associated species are available. Road verges constitute a very common type of semi-natural habitat, where it may be very abundant, or present only as an occasional species. The following list is typical of such a community on clay soil:

<i>Allium vineale</i>	l.ab.	<i>Festuca ovina</i>	f.
<i>Arrhenatherum avenaceum</i>	v.ab.	<i>Potentilla repens</i>	f.
<i>Dactylis glomerata</i>	v.ab.	<i>Trifolium pratense</i>	f.
<i>Lathyrus pratensis</i>	ab.	<i>Heracleum sphondylium</i>	f.
<i>Medicago lupulina</i>	ab.	<i>Cirsium arvense</i>	o.
<i>Plantago lanceolata</i>	ab.	<i>Centaurea nigra</i>	o.
<i>Ranunculus acris</i>	ab.	<i>Senecio jacobea</i>	o.
<i>Achillea millefolium</i>	f.	<i>Crepis virens</i>	o.
<i>Vicia sepium</i>	f.	<i>Tragopogon pratensis</i>	o.
<i>Taraxacum officinale</i>	f.	<i>Rumex crispus</i>	o.
<i>Trifolium repens</i>	f.	<i>Phleum pratense</i>	o.
<i>Lolium perenne</i>	f.	<i>Poa pratensis</i>	o.
<i>Convolvulus arvensis</i>	f.	<i>Plantago major</i>	o.
<i>Plantago media</i>	f.	<i>Lotus corniculatus</i>	r.

On arable land occurrence may be sporadic and of a low frequency, but the density may rise to over 30 plants per square foot (0.1 m.<sup>2</sup>). Variations in frequency in various habitats are shown in the following table.

Table 3. *Relative abundance of Allium vineale in different habitats*

(All figures obtained by sampling within infested areas of particular fields)

Locality	Description of site when counted	Soil type	Date of count	Density per sq.ft. (0.1 m. <sup>2</sup> )	Proportion of scapigerous plants (%)
Cambridge Univ. Farm	Ley since 1940	Gault	Sept. 1941	2.3	—
"	"	"	April 1942	3.6	—
"	"	"	"	5.3	—
"	"	"	"	5.2	—
"	Beans after wheat	"	Mar. 1942	4.2	—
Madingley, Cambs.	Fallow after wheat	"	Mar. 1943	34.4	—
"	"	"	April 1943	32.4	20.8
"	"	"	May 1943	22.0	31.5
Trumpington, Cambs	Road verge	Chalk	April 1942	7.6	33.7



*Allium vineale* L.

Typical associated weeds and their relative frequency are indicated by an analysis of grain used as horse fodder taken from an infested field at Orwell, Cambs: the sample weighed 218 gm., 212 gm. of which were seeds of the fodder crop (a mixture of oats and wheat), with grass weeds. The remaining 6 gm. contained (analysis by A. P. Conolly):

<i>Allium vineale</i>	326 bulbils	<i>Peucedanum sativum</i>	7 seeds
<i>Sinapis arvensis</i>	113 seeds	<i>Rumex</i> sp.	5 „
<i>Ranunculus arvensis</i>	37 „	<i>Lithospermum officinale</i>	4 „
<i>Scandix pecten-veneris</i>	33 „	<i>Aethusa cynapium</i>	1 „
<i>Galium aparine</i>	11 „	<i>Allium ? vineale</i>	1 „
<i>Lychnis githago</i>	10 „		

Another list shows the transition in the associated weed flora in a cultivated field, the upper part of which lies on gravel and the lower on gault:

Species	Upper region (sand and sandy loam)	Middle (clay loam)	Lower (clay)
<i>Allium vineale</i>	r. (1 specimen)	o.	f.
<i>Alopecurus agrestis</i>	v.ab.	v.ab.	v.ab.
* <i>Matricaria inodora</i>	v.ab.	o.	—
* <i>Veronica persica</i>	v.ab.	v.ab.	ab.
* <i>Cirsium arvense</i>	v.ab.	v.ab.	o.
<i>Senecio vulgare</i>	ab.	ab.	ab.
<i>Plantago media</i>	f.	f.	f.
* <i>Capsella bursa-pastoris</i>	f.	—	—
<i>Myosotis arvensis</i>	f.	f.	f.
<i>Scandix pecten-veneris</i>	f.	—	—
<i>Polygonum aviculare</i>	f.	—	o.
* <i>Stellaria media</i>	f.	o.	o.
<i>Tussilago farfara</i>	l.ab.	—	—
<i>Lychnis alba</i>	r.	—	—
† <i>Sinapis arvensis</i>	o.	v.ab.	v.ab.
<i>Chenopodium album</i>	o.	o.	o.
† <i>Sonchus asper</i>	o.	f.	f.
† <i>Linaria spuria</i>	o.	f.	f.
<i>Taraxacum officinale</i>	o.	—	o.
† <i>Anagallis arvensis</i>	o.	f.	f.
<i>Veronica agrestis</i>	o.	—	—
<i>Galium aparine</i>	o.	f.	o.
<i>Papaver rhoeas</i>	r.	—	—
<i>Cerastium vulgatum</i>	r.	—	—
<i>Arenaria serpyllifolia</i>	r.	—	—
<i>Aethusa cynapium</i>	r.	—	—
<i>Caucalis anthriscus</i>	r.	—	—
† <i>Euphorbia exigua</i>	—	f.	f.
† <i>Atriplex hastata</i>	—	o.	f.
<i>Pieris echinoides</i>	—	o.	o.
<i>Equisetum arvense</i>	—	o.	—
<i>Polygonum convolvulus</i>	—	—	o.
<i>Plantago lanceolata</i>	—	—	r.
<i>Lithospermum officinale</i>	o	—	—

\* Indicates species showing frequency changes parallel to that of *A. vineale*.

† Indicates species showing the reverse tendency.

The left-hand column in this list refers to soil types closely similar to those given in samples 6 and 7 of Table 2; the central column to samples 3, 4 and 5, and the right-hand column to samples 1 and 2.

IV. *Response to biotic factors.* (This section can only be appreciated when the facts of the morphology and life-cycle outlined in VI and VII have been studied.)

As an agricultural weed, extraordinarily resistant to any form of artificial disturbance, such as ploughing, grazing, etc.

(a) *Ploughing.* Effect depends on time of ploughing relative to the development of the

plant, and also, possibly on the nature of the soil. The heavy soils on which the species is most abundant are generally winter sown and ploughed before, or not long after 'germination'\* of the bulbs has set in. Smaller plants uprooted and left on the surface may be killed, but in others sufficient food reserve is still present in the bulb to enable the plant to be re-established. Winter or spring ploughing may be much more effective as the plants are then uprooted when the reserves are largely depleted and resistance is lower: a critical period of short duration occurs in the life-cycle, usually in mid-February, although not coinciding throughout the population, when the fleshy scale of the parent bulb is exhausted, and the laying down of food storage tissue in the transient or terminal bulb has not commenced. Ploughing performed at this time is most effective. Lighter soils are generally ploughed later in the season than the heavy ones, and spring sown, and are much less liable to infestation by the wild onion even where this is prevalent in the vicinity. How far this is an edaphic response rather than a biotic one has not been satisfactorily determined.

Ploughing affects only growing plants and a large proportion of the total population is always present in the form of dormant bulbs. Hence spring cultivation when employed as a method of control must be continued over several years. Tinney (1942) requires six years for his method; that recommended by the United States Department of Agriculture (Talbot, 1929) requires three years.

Late ploughing, as in bare fallowing, also prevents bulbil formation, and the response of the plant to summer fallowing has been investigated by R. Garrett-Jones of the Grassland Improvement Station, Dodwell Drayton, Warwickshire: an early crop such as barley or rye is grown, and the land ploughed as soon as possible after the crop is off. It is left fallow, reploughed the following May, and two or three times subsequently. Bulbil production is thus eliminated and earlier germination of the bulbs appears to be encouraged. Autumn ploughing at the usual season then destroys a larger proportion of growing plants. The mid-May ploughing in this system would appear to destroy numbers of immature major offset bulbs and will probably separate minor offsets from the parent plant before the outer scale has hardened. Dormancy will then be inhibited,† and in the following autumn most components of the population which normally have a prolonged germination period (minor offsets and bulbils) will be absent, the major offsets and terminal bulbs usually germinating early, and hitherto dormant minor offsets earliest of all.

(b) *Other cultivating operations.* Growth of cultivated crops such as potatoes, Brussels sprouts, beans or root crops, all assist in eradication as the ground can be disturbed at all seasons, and such cultivation is recommended in a prolonged course of treatment in connexion with spring ploughing, such as that advocated by Tinney (1942). In such crops the onion is noticeably restricted to the rows of the crop plant where it is undisturbed by intertilling operations.

(c) *Cutting and grazing.* Grazed by farm stock during the earlier part of its growth and is a fodder which taints both milk and meat, but repeated nibbling of the foliage appears to have no injurious effect on the plant. Later in the season, when the young scape might be removed, the plant is apparently avoided by grazing animals.

\* This term is used throughout to denote the sprouting of the bulb.

† This has been demonstrated experimentally on a small scale by planting minor offsets detached from the parent plants at the end of May; all germinated with the exception of a few which rotted, none remaining dormant.

No exact information available on the effect of repeated cutting in the field, as in leguminous fodder crops. This is employed as a method of control, but it is not clear how far the effect is due to cutting and how far to other factors, e.g. is a smothering effect. Small-scale experiments on repeated cutting of the foliage down to the ground during the spring have shown that the treatment does not destroy the plant although the increase in bulb weight (i.e. the increase in fresh weight of bulbs and offsets at the end of the season over that of the bulb originally planted) is less than normal, and in larger bulbs there may even be a decrease in weight. (The bulb weight increase has been found to be always less the greater the weight of the original bulb.) Proportion of plants producing aerial scapes unaltered, except for a very slight reduction in the smallest bulbs; production of offset bulbs unaffected.

Decapitation of the scape prior to maturity increases size of offsets to nearly three times normal when performed immediately the scape emerges in mid-May; where later, this increase is proportionally less. In minor offsets increase in size leads to splitting of the outer scale in a far larger proportion, which can thus germinate in the same season. When cut after the spathe has burst, the head of bulbils continues to develop and these can ripen even detached from the parent plant.

(d) *Burning*. Paring and burning the surface layers of soil containing the bulbs has been cited by Long (1931) as a method of getting rid of a dense infestation on a small area of grassland.

(e) *Pulling*. Hand pulling only succeeds in uprooting the bulb if performed at a certain season: at other times the foliage or the scape is generally broken and the bulb remains in the soil. Attempts at removing the bulb by this method, which is only efficacious for scapigerous plants, gave success varying from 32% in July to a maximum of 92% in July when the spathes are just bursting.

(f) *Manuring and draining*. These have an indirect effect on the plant in practice, as they are both means of lightening a heavy soil, rendering it more suitable for spring sowing.

V. (a) *Gregariousness*. Habit distinctly gregarious when growing in undisturbed places, e.g. road verges, where clusters of several small compact clumps each containing half a dozen or more plants are commonly seen. In arable land or pasture distribution more scattered, but the plant often gives the appearance of having spread outwards from one or more distinct centres of infection. Bulbils usually fall from the head together and germinate in very dense patches.

(b) *Performance in various habitats*. Grows most vigorously where freest from competition with other species, e.g. fallow land or waste ground in the vicinity of hay ricks, etc. Cultivated crops such as broad beans permit fairly vigorous growth: in such situations the scape is usually 2–3 ft. (0.5–1 m.), the bulbils fairly large and numerous, with leafy filaments attached. Major offsets up to 2 cm. diameter and minor offsets proportionally large. In cereal crops height may be greater, being usually related to the height of the crop; the heads smaller and more compact; bulbils smaller, but not necessarily fewer, more commonly lacking the leafy filament; offset bulbs considerably smaller. In permanent grassland the plant may apparently disappear after a period of years, and there is evidence that suppression may likewise be induced by growing smother crops. Vigour of the plant on road verges very variable, but never quite as great as on open ground; in dry places habit usually more spindly, with small compact heads bearing smaller and less numerous

bulbils, and a lower proportion of scapigerous plants in the population than elsewhere: no difference in the tendency of these to bear flowers observed in the different habitats. The factors determining the type of development undergone by each plant (i.e. whether it will become scapigerous or form a terminal bulb) may be largely environmental, but their nature is unknown.

(c) *Effect of frost, drought, etc.* Extremely frost-hardy; no permanent damage observed even after many weeks' intensive frost: growth-rate as measured by elongation of leaves reduced to practically nil and foliage dies back from the tip, but growth is renewed rapidly as soon as thaw sets in, leaves which have died right back elongating from the base.

Drought impoverishes the plant and reduces the tendency to scape production. Dormant bulbs extremely drought resistant and even growing plants can recover after being uprooted by the plough and left to dry out on the soil surface. Experimental plants kept in waterlogged soil throughout the growing season were found to be quite capable of normal growth.

#### VI. (a) *Morphology of underground parts.*

*Bulb types* (Fig. 4). (i) Offset bulbs: of two types, the 'major' which develops in the axil of the innermost leaf of the parent plant, and the 'minor' offsets which develop in the axils of the outer leaves. Both consist of a single fleshy bulb scale, surrounded by an outer protective scale. Major offsets ovate in longitudinal section, somewhat longer than broad, and 0.5–2.0 cm. in diameter, with a convex abaxial face meeting the flat adaxial face forming two distinct ridges which clasp the sides of the flattened scape base to a slight extent (Fig. 2 B). Semicircular attachment scar at the base of the adaxial face. Outer scale with acuminate tip, light buff, glossy and fibrous, with longitudinal splits at maturity; of a brittle papery texture, but of great durability. Minor offsets similar in shape, but smaller and diameter proportionally less. Length may attain 2 cm. but majority are between this and 1 cm. Outer scale tougher, darker in colour, usually intact at maturity, with a sharp terminal point and prolonged at the base into a curved stalk, terminating in the attachment scar. This stalk is longest in the offset in the outermost leaf axil, shortest or lacking in the innermost.

(ii) Terminal bulb (Fig. 2 C): structure essentially similar to that of offsets although outer scale sometimes lacking and the bulb invested only in withered foliage leaf bases. If present, outer scale resembles that of the major offset, and is similarly prolonged into a sharp terminal point. Size very variable, but never as large as largest major offsets. Bulb circular in cross-section, with a circular attachment scar at the base. Frequently accompanied by one or two minor offsets which develop in the axils of the ensheathing foliage leaves.

(iii) Transient bulb (Fig. 5): this term is applied to the layered bulb which results from the swelling of the foliage leaf bases during early spring, and is a condition of only short duration, giving place to the terminal bulb or, in the final season of development, to the offset bulbs and scape. Not more than two or three leaf bases are swollen simultaneously in the transient bulb, the outer ones being depleted as the inner ones develop.

*Root system.* Roots are white, unbranched, or very rarely branched, and fine, although coarser contractile roots (cf. (b) below) may be present. Root hairs abundant, extending

from 1 to 10 cm. from the base of the roots, but only along 2–6 cm. of any particular root; additional root hairs may be present just behind the root tip. Disposition of the roots characteristic of the bulb type from which they spring: in major offsets and terminal bulbs 30–50, later increasing to 50–100 roots develop, forming at first, in the former,

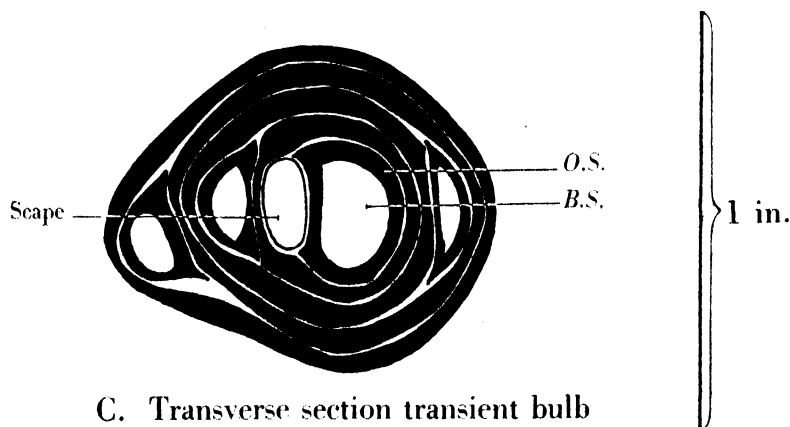
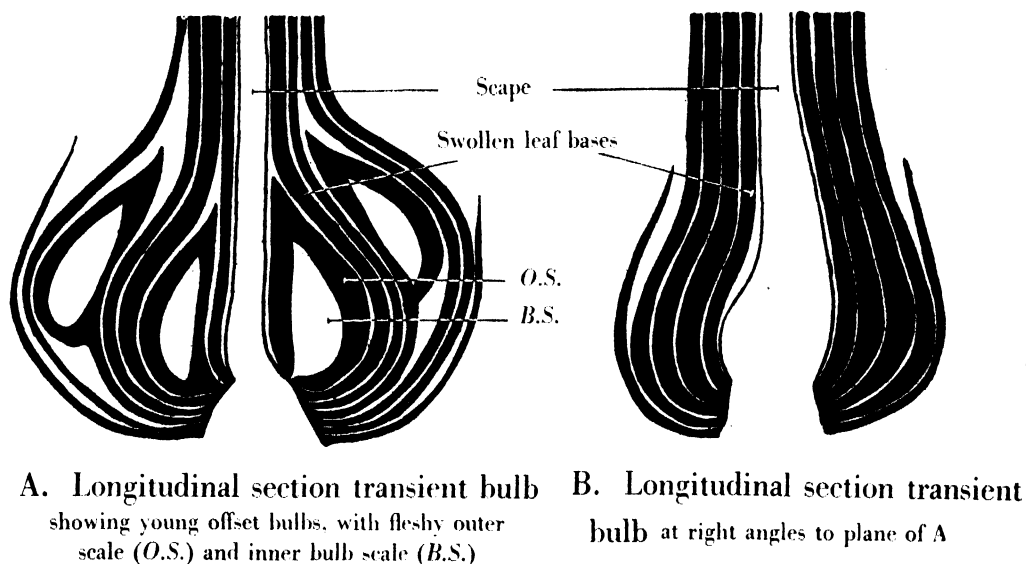


Fig. 5.

a semicircle round the curved abaxial edge of the attachment scar, and in the latter a complete ring round the base of the bulb. In smaller specimens roots are fewer, while in minor offsets there are only four or five, these emerging from the base of the bulb, not in the region of the attachment scar. In bulbils only two or three roots usually develop, from the base of the bulb.

(b) *Depth, etc. of underground stem and roots.* Depth of bulb in natural state difficult to determine owing to the prevalence of the plant on arable land where bulbs are displaced by cultivation. Generally most abundant from 2 to 6 cm., being less frequent above this

level and extending with diminishing frequency to about 15 cm. Elongation of the stem of the bulb during the growing season may account for some slight change in depth, and soil contraction, particularly the deep fissuring of clay soils during the summer months, may cause further displacement of the bulb. The latter may well account for the records of growing bulbs at depths of 3 ft. (1 m.) on arable land on gault clay. Superficial bulbs within 2–3 cm. of the soil surface show definite depth adjustment by means of contractile roots, accompanied by transverse wrinkling, particularly of the coarser roots, over 1–2 cm. at their base. The bulbs may be drawn down as much as 1·5 cm. by this process, depending to some extent on the nature of the soil or on the size of the bulb: where the bulb is small and there are only two or three roots present these are usually vertical, an arrangement which, together with the small size of the bulb, presumably facilitates movement. Mechanism of depth perception not known.

Direction of growth of roots more or less vertical after an initial sloping out from the base of the bulb. Root length at least 30–50 cm. in larger bulbs; maximum length in the field not known.

(c) *Mycorrhiza*. (Report by M. C. Rayner on material from Madingley, Cambs; examined in April 1946.) The whole root system is mycorrhizal; in effect all roots are mycorrhizas.

The association is endotrophic with a member of the 'vesicular-arbuscular' group. The mycelium is intercellular and intracellular in distribution affecting the whole of the cortical tissues. Large pear-shaped vesicles occur, but typical intracellular complexes (arbuscules) are not yet present owing doubtless to the relatively immature stage of growth.

(d) *Perennation*. Bulb geophyte. Quiescent period of the life cycle extends from May to September, and dormancy most complete during July and August. Perennation by means of four types of bulb; the majority of smaller individuals perennate as terminal bulbs, formed around the growing point as explained above. The scapigerous plant produces perennating organs of three types, the major and minor offset bulbs below ground, and the bulbils above. The latter (Fig. 4) are small, ovoid or obovoid structures, often somewhat angular in cross-section owing to contact faces formed during development on the compact head, surrounded by other bulbils on all sides. Structure fundamentally the same as in other bulb types, the outer scale thin and papery, sometimes terminating in a leafy filament of a few centimetres long.

At maturity each perennating bulb contains two or three incipient foliage leaves enclosed in the fleshy scale, the growing point being distinguishable at the centre of these, the most important difference between the various types lies in the nature of the outer scale. In the bulbils it is thin and papery, readily separating from the ripe bulbil in the region of the attachment scar. In the major offset and, when present, in the terminal bulb, it is similar but rather thicker, readily detachable from the base of the mature bulb, and splitting lengthwise in one or more places as this ripens. In the minor offsets the outer scale is considerably thicker and in the majority remains unsplit even in the ripe bulb. The attachment scar where, in other types, the roots break through on germination, is in this case at the end of a short curved stalk, and the roots break out at some distance from it. This outer scale causes the frequently prolonged dormancy of the minor offset bulbs. About 50% remain ungerminated in the soil for two years, the maximum period of dormancy being probably about six years. The conclusion that prolonged dormancy is due

to the nature of the bulb scale is borne out by experiment and by the fact that it does not occur where this scale is split, either naturally or artificially, and also by the detailed structure of the scale. In all cases it is heavily cuticularized, and has a waxy, non-wettable surface. In the fully ripe condition the cell walls are very strongly lignified, giving a structure which must be practically impervious: this most pronounced in the minor offsets, but only slightly less marked in the other types. Hence it is believed that germination can only take place when this scale is split or detached at the base, which happens invariably in all but the minor offsets as soon as the bulb is ripe.

As germination takes place from the end of August onwards, the plants are seen during the winter months with 2-4 foliage leaves, and from a few to 10 cm. tall. Small plants are frequently seen with a single leaf thrown into one or more spiral coils.

(e) *Vegetative reproduction.* Reproduction almost entirely vegetative, at any rate in this country. Most rapid multiplication is by means of bulbils produced in large numbers (up to 300) on head of scapigerous plant. These are roughly the size of wheat grains and ripen at the same time, so that when the plant is present in a cereal crop these bulbils are readily disseminated in grain used as seed, and also in straw. Transmission by wind or other agents unlikely to carry bulbils more than a short distance, but abundance of the plant on road verges may well lead to direct infection of adjacent fields. The bulbils in the year following germination produce a small terminal bulb, perhaps with one or two minor offsets.

Scapigerous plants also multiply below ground, each producing a single major offset, with 1-4 minor offset bulbs. These in turn germinate, producing either terminal bulbs, with or without minor offsets, or new scapigerous plants. These underground reproductive bodies are not known to be spread from one place to another by any natural agency, though they may well be transmitted on agricultural implements, on the feet of cattle, etc.

Numerically the bulbils are clearly the most important means of spread, and their importance in maintaining the population appears even greater when the high mortality of the underground bulbs due to fungal infection, described in IX (c) below, is taken into account.

(f), (g) *Longevity of the individual plant and age at first flowering.* In a sense the life of the individual plant may be said to terminate with the production of the bulbil bearing scape, with or without flowers, the offset bulbs replacing the parent bulb below ground, but these newly formed individuals take varying lengths of time to reach the scapigerous stage; one season suffices the majority of major offset bulbs and many of the minor offsets, while others of the minor offsets reach this stage within a single season of germination, although this may be several seasons after their formation. The bulbils take a minimum of two seasons after germination to reach the scapigerous stage and experimental data on the actual length of time taken are as follows:

An initial sample of 112 bulbils produced in the summer of 1941 and planted in the same autumn produced 12.5% scapigerous plants in 1943; a further 58% in 1944, making a total of roughly 70% in three years. By 1945, 91% had reached maturity.

Bulbs not reaching the scape-producing stage produce terminal bulbs at the end of each season of their growth. The line of development is determined early in the growing season, but is not correlated solely with bulb size.

(h) *Frequency of seed production.* Uncommon in this country, but fruiting specimens

recorded from Herefordshire (Herb. Babington in Cambridge Botany School) and east Hertfordshire (H. W. Pugsley).

(i) *Ecotypes*. No information.

(j) *Chromosome number*.  $2n=32$  (Mert. Cat.).

VII. *Phenology* (Figs. 3, 4). Timing of the developmental cycle differs somewhat in the production of the scapigerous plant or in that of a terminal bulb from a small bulb, or again in the case of growth from a bulbil, and even within these categories, owing to the prolonged germination period, there is considerable variation. Nevertheless, the life cycle as observed in Britain can conveniently be divided into three periods:

(1) August–February: period of germination and exhaustion of the parent bulb.

(2) March–April: transient bulb stage, with initiation of terminal and offset bulbs.

(3) May–August: period of development of the head and maturation of scapigerous plants; terminal bulbs mature, ripen and become dormant.

The timing of events appears to be different on the Continent (Lebensg. 3).

(a) Germination commences in the major offsets and terminal bulbs in September, but takes place principally in October and November; that of the minor offsets may coincide, or, in the case of bulbs that have been lying dormant over the previous one or more seasons, occurs predominantly towards the end of August. Germination of bulbils generally commences in November, and continues until January.

From commencement of germination onwards there is a gradual depletion of the fleshy bulb scale, which becomes progressively more shrivelled as development proceeds. Complete exhaustion occurs on the average during the latter part of February, but depends on the time of germination of the individual and on its size. At the same time foliar elements are cut off in succession round the growing point inside the bulb, and up to five, in addition to the first sheathing leaf, have been initiated by the end of the first period of development in the case of those plants which will become scapigerous in the current season. Where the production of a terminal bulb is to mark the end of the season's growth, rarely more than three leaves, in addition to the first sheathing leaf, develop round the growing point during this period. Thus the type of development which will take place can be fairly safely predicted at an early stage.

The second period is that of most rapid developmental changes, following immediately on the exhaustion of the fleshy scale. In the scapigerous plant the bases of the outer two or three foliage leaves, sometimes also with that of the first sheathing leaf, become swollen and fleshy, producing the transient bulb. This stage is reached by mid-March and the bulb may later enlarge considerably, the leaf bases swelling to as much as 2.5 mm. in thickness. Offset bulbs begin to develop towards the end of March, but the major offset does not appear until two or three weeks later. Elongation of the central axis begins at about the same time, the young scape having grown up within the sheath of the innermost leaf for about 5–10 cm. by the end of April.

During the early stages of its development the offset bulb consists of a small fleshy scale surrounded by an outer scale which is also thick and succulent. The bulb enlarges steadily from the time of its formation, while the outer scale loses its succulent character and hardens during May into the tough investment of the ripe bulb; by the end of this month the minor offsets have usually reached their full size. The major offset matures later, the outer scale not hardening until late June.

These maturation processes take place during the third period of development and are



accompanied by a progressive shrivelling of the swollen leaf bases of the transient bulb: this proceeds fairly slowly during May, but then rapidly, being complete by the end of July.

In plants producing terminal bulbs the second period of development often commences rather earlier than in the scapigerous plants, as the latter are, on the whole, larger, and the fleshy scale is less rapidly exhausted. The initiation of the terminal bulb follows closely on the exhaustion of the old fleshy scale, and has been observed as early as January. It has taken place in the majority by the latter part of February, the original bulb usually being exhausted early in this month. The production and maturation of the minor offsets is correspondingly earlier, and by mid-May both these and the terminal bulbs are practically fully grown. Very little enlargement of the foliage leaf bases ever occurs, any appearance of a layered bulb being even more transient than in the scapigerous plant.

Roots produced on germination elongate rapidly to 30–50 cm., and root hairs are well developed within a fortnight of germination; these later become very abundant, developing behind the elongating portions of roots within a week of their formation. Actual rate of elongation of roots and exact period of maximum elongation not known. Roots increase gradually in number in larger bulbs, particularly during the second period of development, having successively higher points of origin on the base of the bulb. In these the later formed roots are frequently coarse and contractile, and although in the smaller bulbs the number is not much increased, one or two such roots may develop some time after germination if the bulbs are superficially placed.

Root contraction may occur earlier in some cases, but in superficial bulbs is fairly widespread by December, becoming more pronounced during January and February.

During the third period of development there is no further change in the root system except for a gradual withering away, the roots being quite shrivelled by the time the scape is ripe.

(b) Appearance of new leafy shoots follows appearance of roots on germination at the times given in (a) above, being delayed slightly according to the depth of the bulb in the soil. Precocious development of bulbs and bulbils is of fairly frequent occurrence. In April the outer scale of minor offsets, which is at that time thick and succulent, may elongate apically into a flattened foliage leaf, and one or two further leaves may be present between it and the fleshy scale, producing a small axillary shoot beside that of the main plant. At maturity such bulbs rarely show any difference from normal minor offsets, but occasionally they may produce aerial scapes with bulbils, and a series of offsets below ground (Fig. 6). A similar precocious development is also sometimes observed during June and July in the bulbils. Here the outer scale is very commonly prolonged into a leafy filament of a few centimetres in more vigorous individuals and in heads where only a few larger bulbils are present. In the latter an additional leaf may develop round the fleshy scale and minute bulbs of the minor offset type may be produced in the leaf axils, the ripe bulbil becoming a small terminal bulb.

(c) Flowers July–August. Flowers are usually in bud when the spathe bursts in mid-June.

(d), (e) No information on time of ripening, shedding and germination of seeds.

VIII. (a) *Mode of pollination of flowers.* Flowers strongly protandrous; stamens of inner whorl elongate first, followed by those of outer. Style becomes exerted after anthers have withered. Rich in nectar collecting at the base of the perianth (Lebensg. 3).

(b) *Insect visitors*. None recorded in Britain; only humble-bees and Muscidae can effect cross-pollination (Lebensg. 3).

(c)–(k) *Cleistogamy, Apomixis, Vivipary*. No information.

(l) Reproduction by seed of negligible importance in Britain; the same probably the case on the Continent (see above VI (e) and (h)).

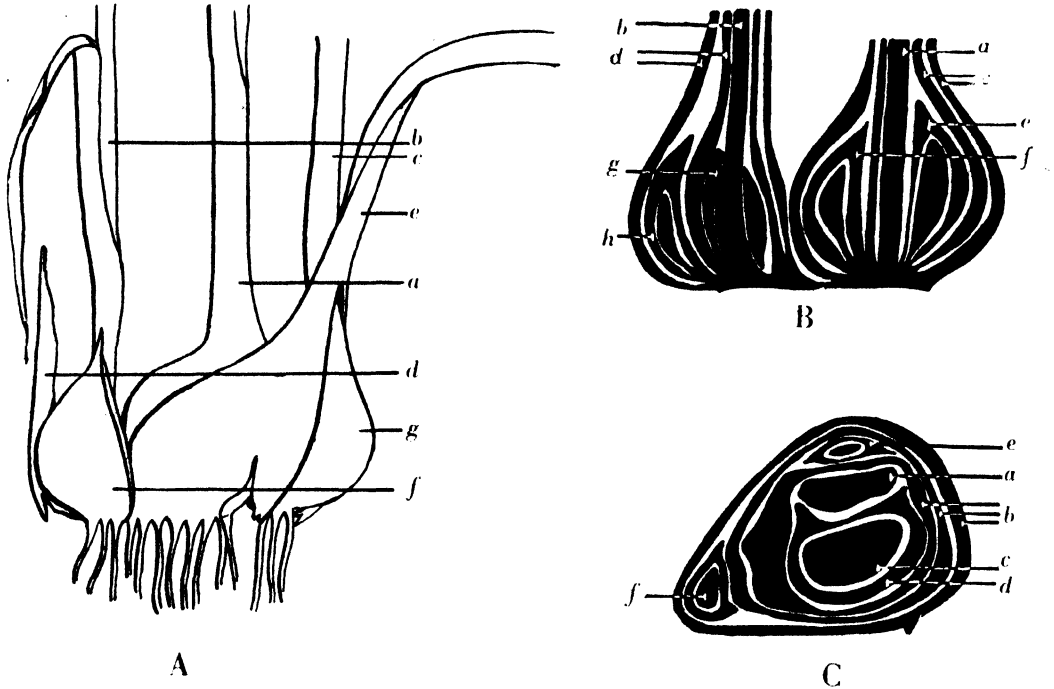


Fig. 6. A. Scapigerous plant as found in May with two precocious minor offsets each producing a subsidiary scapigerous plant (slightly reduced). *a*, scape of parent plant; *b*, *c*, lateral scapes; *d*, base of first foliage leaf; *e*, 2nd foliage leaf; *f*, precocious offset in axil of 1st foliage leaf. B. L.S. through parent plant shown in A with precocious offset in axil of 1st foliage leaf ( $\times \frac{1}{2}$ ). *a*, scape of parent plant; *b*, scape of precocious offset; *c*, foliage leaf bases; *d*, foliage leaf bases of offset; *e*, major offset; *f*, normal minor offset; *g*, major offset produced by plant from precocious offset; *h*, normal minor offset produced by plant from precocious offset. C. T.S. through precocious offset in axil of 2nd foliage leaf ( $\times 1$ ). *a*, scape; *b*, foliage leaf bases; *c*, major offset; *d*, outer scale of major offset; *e*, *f*, minor offsets.

IX. *Parasites, diseases, etc.* (a) *Animals feeding on the plant*. Grazed by farm stock and probably by rabbits and mice; bulb tissues eaten by slugs (*Agriolimax agrestis* L.) and underground parts also attacked by millipedes. The eelworm, *Anguillulina dipsaci* Kühn, is recorded from Holland, and species of Enchytraeidae are saprophytic on decaying bulb tissues. No insect parasites are recorded.

(b) *Plant parasites*. The following fungi occur parasitically: *Penicillium* sp., *Fusarium* sp., *Sclerotium cepivorum* Berk., *Sclerotium* sp. (unidentified), *Urocystis* sp. (not *U. cepulae* Frost, Moore, 1943), '*Caeoma alliorum* Link' (Plowright, 1889).

(c) *Serious diseases*. Rotting of young bulbs by *Penicillium* and *Fusarium* of frequent occurrence from July onwards. *Penicillium* the more frequent, causing widespread destruction of the bulbs, although partially rotted bulbs frequently germinate and become established.

\* '*Caeoma alliorum* Link' is the name formerly given to the caeomatal stage of several species of *Melanospora*.

*Botrytis*, *Sclerotium* sp. Dark convoluted sclerotia commonly found on underground parts of the plant from July onwards, often destroying all the young offset bulbs, the major offset, where the outer scale is still succulent, being the most susceptible: minor offsets protected to some extent by the outer scale, particularly where this is intact. Spore producing mycelium observed once only, in June 1943, following a period of unusually warm, damp weather: young scapes, particularly those of the smaller scapigerous plants, were invested with a superficial mycelium, causing rotting and collapse before the bulbils were ripe: the latter, however, in many cases, although undersized, ripened on the shrivelled scape. In this same season sclerotia were found on about 50% of the plants pulled up by the scape in mid-July: an even greater number of scapes were rotted at the base and came up without offsets attached, but bearing traces of sclerotia. The great majority of these showed no sign of damage to their overground parts.

*Sclerotium cepivorum*. In early stages of infection a fine white mycelium covers the surface of the bulb, followed in July by black, shot-like sclerotia filling the cavity left by the rotting offset bulbs within the withered foliage leaf bases. Infection probably through the roots as in other species of *Allium*. No trace of infection or damage observed above ground. As with *Botrytis*, the major bulb is most readily attacked. The incidence of *Sclerotium* may be as great as that of *Botrytis* and the two may occur together on the same plant. Both pathogens only noted so far where the plant is present on heavy clay soil, but have been found alike on arable and fallow land and in young leys. Both evidently take a high toll of the offset bulbs, at least in certain seasons, a fact which increases the significance of the role of the bulbils in the maintenance of the species, and accordingly adds to the desirability of controlling bulbil production where the plant is prevalent as a weed.

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## BRITISH ECOLOGICAL SOCIETY

### ANNUAL MEETING IN THE UNIVERSITY COLLEGE, EXETER

JANUARY 1946

The Annual General Meeting of the Society was held in the Washington Singer Laboratories on Friday, 4 January 1946 commencing at 10 a.m.

The minutes of the last Annual General Meeting were read and signed, and apologies for absence were received from Dr E. Wylie Fenton, Dr H. Godwin, Mr F. R. Horne, Prof. W. H. Pearsall, Sir E. J. Salisbury and Dr W. B. Turrill.

The following were elected to membership of the Society: A. R. Boughey, H. R. Hewer, D. P. W. McCarthy, K. R. Ashby, H. G. Baker, E. N. Buxton, P. J. Wanstall, P. E. Glover, J. Bovill, B. Campbell, J. H. Day, J. Hobart, E. B. Brown, H. E. Hornby.

The report of the Hon. Secretaries upon the work of the Society in 1945 was read and approved, Prof. Osborn moving and the meeting carrying a vote of thanks to the Secretaries for their services through the year.

#### *Report of the Hon. Secretaries for the year 1945*

The thirty-first Annual Meeting of the Society was held in the University School of Botany, Cambridge on 9 and 10 January 1945. The meeting opened on the afternoon of 9 January with an exhibition of ecological material in the large elementary laboratory. In the evening a large number of members and guests were entertained at a soiree in the Combination Room of Clare College, very kindly placed at the service of the Society by the Master and Fellows. The business meeting of the Society followed next morning at 10 a.m., and was succeeded by the reading of the Presidential address upon 'Ecology from the Standpoint of the Entomologist', and by four other ecological papers. The Society is much indebted to Prof. Brooks and his colleagues for having given the hospitality of the Cambridge department so generously and successfully.

It has again proved impracticable to hold a Summer Meeting of the Society, but it is hoped to restore the pre-war practice in 1946 with a summer meeting in Sheffield.

The retardation of publication of our journals has continued but the second part of each journal is in the press and should appear soon. The 1945 volume of *The Journal of Ecology* will contain in its two parts fifteen original articles, together with reviews and parts of the Biological Flora: in all the volume will contain about 320 pages. Volume 14 of *The Journal of Animal Ecology* will be of about 180 pages, containing eleven original articles, as well as notices, reviews and the usual full series of notices of publications on the animal ecology of the British Isles.

Publication of the Biological Flora continues satisfactorily with the appearance of accounts of the genus *Polygonum*, three of its species, *P. persicaria*, *P. lapathifolium*, *P. petecticale*, and of *Gentiana pneumonanthe*. Prof. Clapham has prepared, and there is standing in type a new check list of British Flowering plants for use in connexion with the Biological Flora.

In the current volume of *The Journal of Ecology* appears the sixth and final report on the Society's Transplant Experiments at Potterne, carried out with such fidelity and success by Mr Marsden-Jones and Dr Turrill.

With the amelioration of paper rationing and better labour supplies we look forward to a restoration of the journals to their pre-war size and form, a return especially welcome in view of the editors' desire to publish the excellent articles which reach them in good numbers both from home and overseas.

The instruction to the Council given by the last Annual Meeting was followed by the compilation and printing of a special memorandum upon 'The Establishment of an Aerial Unit for Scientific Work'. This was suitably distributed and attracted considerable attention, and a government committee has now been set up to consider this matter.

Following publication in the journals of the report on 'Nature Conservation and Nature Reserves' the Council of the Society prepared and issued to members and to a large number of appropriate journals

and institutions a second and shorter 'Memorandum on Wild Life Conservation and Ecological Research from the National Standpoint'. In this were set out the Council's considered views on the national organization most likely to achieve the proper protection, study, use and enjoyment of native plant and animal life. Both report and memorandum have been placed before the National Parks Committee (appointed by the Ministry of Town and Country Planning) and its Wild Life Conservation Special Committee.

Members of the Society should realize the great debt we owe to the Council members who bore the brunt of the heavy task of framing, amending and issuing these reports and memoranda.

As evidence of the remarkable way in which our members on active service have retained their vivid interest in ecological matters we may mention the very interesting series of reports sent to the Society of the activities of the Middle East Biological Scheme under which service members pursue usefully directed field studies on plant and animal life.

During the year the membership of the Society has risen from 420 to 458 members, 23 members have resigned or died, and 61 new members have been elected. Of the present membership 229 receive *The Journal of Ecology* alone, 139 *The Journal of Animal Ecology* alone, 85 take both journals, and 5 are Associates receiving neither. The membership of the Society, which was 363 in January 1939, suffered inevitable setbacks through war difficulties: in 1940 there was a fall in membership to 335, but since then recovery has been remarkably rapid to our present total of 458. We are happy to see this indication of the vigour of the Society.

We regret to announce the death during the year of our distinguished members, Prof. R. Sernander and Dr Boris Keller, and the resignation of Prof. Sir R. G. Stapledon and Prof. G. D. Fuller.

H. GODWIN } *Hon. Secretaries,*  
L. A. HARVEY } *2 January 1946*

The President proposed that Prof. Sir Edward Salisbury, F.R.S., be congratulated upon having received the Gold Medal of the Royal Society, and upon having received the honour of Knighthood: this was carried with acclamation.

Dr V. S. Summerhayes presented a provisional report on the financial position of the Society. He pointed out that the comparatively large reserve accumulated during the past few years must be regarded as at least partly temporary, and due to be expended as soon as paper and labour supplies allow the journals to resume normal publication. He concluded by moving that a grant of £10 be made as in former years to the Freshwater Biological Association. The report and resolution were accepted, and on the motion of Dr E. W. Jones, the Hon. Treasurers were thanked for their remunerative labours in the past year. It was moved and agreed that Messrs Wm. Norman and Sons be reappointed auditors to the Society.

A letter from Prof. W. H. Pearsall was read, in which he pointed out that the increased allocation of paper could not become effective until late in the year, owing to labour shortage, and that printing costs would then have risen by between 30 and 50 %. It was proposed to keep *The Journal of Ecology* in its present form throughout at least the next volume. It was hoped that concise articles would now be published within a year of acceptance, and the desire was expressed to receive further contributions to the Biological Flora.

Mr C. S. Elton reported on *The Journal of Animal Ecology* that articles were coming in rapidly, but that space was not at present restricting publication. Articles had arrived from France and China, and much material was expected to result from the official survey and control work carried through during the war years. In order to publish so much *The Journal of Animal Ecology* must retain its present format, and must be expanded as soon as possible.

These reports on the state of the two *Journals* were accepted and on the proposal of Mr I. Hepburn the editors were cordially thanked by the meeting.

Prof. A. R. Clapham reported that a total of nineteen accounts of species and five of genera had been published in the Biological Flora: some 150 other accounts were promised, and it was requested that finished accounts should be sent to Dr P. W. Richards without delay. Contributors were reminded of the need to send herbarium sheets to the Herbarium of the Oxford University Botanical Department.

Capt. Diver reported that the National Parks Committee and its Wild Life Conservation Special Committee were considering all the various documents submitted to them relative to Nature Conservation.

He indicated the very satisfactory state of affairs that three out of four of the Society's Committee on Nature Conservation were members of the Wild Life Conservation Special Committee, and were able to exert considerable influence on its policy.

The meeting then proceeded to the election of officers as follows:

*President:* A. S. WATT.

*Vice-presidents:* P. W. RICHARDS, C. B. WILLIAMS.

*Hon. Secretaries:* H. GODWIN, A. L. HARVEY.

*Hon. Editors:* W. H. PEARSALL, C. S. ELTON.

*Ordinary Council Members:* A. R. CLAPHAM, H. C. GILSON, I. HEPBURN, A. C. HARDY, G. C. VARLEY.

Mr Harvey gave notice of a joint meeting with the Royal Meteorological Society in London provisionally fixed for the afternoon of 27 March, the subject for discussion to be 'The Influence of Local Climates on Vegetational Distribution'.

Dr Watt, on taking the chair vacated by Dr O. W. Richards, expressed his thanks to the Society for the honour they had done him, and the meeting proceeded to the programme of communicated papers. Miss J. Lambert described 'The Interrelationships of the Chief Plant Communities round the Yare Broads, Norfolk'. She dealt with successional relationships of the dominant species of reed swamp, fen and carr round Surlingham and Rockland Broads. The balance between anchored *Phragmites* reed swamp and *Glyceria maxima* hover was discussed, the *Glyceria* of the Yare broads depending on free access of circulating water, and being an interpolated phase absent elsewhere in the Norfolk Broads. In later stages of the episere alder 'swamp carr' appears to be successionaly related to *Salix atrocinerea* 'fen carr', not genetically distinct from it. A scheme was formulated showing the relationship between *Juncus subnodulosus*, *Glyceria* and *Phragmites* and drainage conditions and past economic utilization of the anthropogenic fen regions where these three species may dominate large areas. To the discussion which followed Dr P. W. Richards, Dr E. W. Jones, Mr C. S. Elton, Prof. A. R. Clapham, Dr A. S. Watt and Capt C. Diver contributed.

Mr B. D. W. Morley, discussing 'The Interspecific Relations of Ants', proposed that such relations may be classified as Casual or Obligatory, Competitive or Non-competitive, or even Co-operative, the obligate competitive relation being further subdivided according as it is intra- or extra-nidal. He summarized the classification he proposed, giving many examples drawn from British species. Mr C. S. Elton, Mr W. H. Dowdeswell, Capt. C. Diver, Dr A. S. Watt, Mr V. S. Summerhayes and Major C. W. Hume took part in the discussion which followed.

Dr W. Watson's contribution on 'Some Devonshire Work' was a brief outline of some problems concerning the distribution of the sessile and pedunculate oaks in the south-west. The predominance of *Quercus robur* in Devon woods, such as those at Wistman's Wood, Holne Chase and elsewhere is anomalous in the light of the apparent preference of *Quercus sessiliflora* (= *Q. petraea*) for heavy rainfall, and demands investigation. This plea was warmly supported by Dr E. W. Jones, Prof. H. G. Champion also speaking on certain of Dr Watson's points.

The meeting then adjourned for lunch, following which, Dr G. M. Spooner read a paper on 'The Distribution of *Gammarus* Species in Estuaries'. He indicated that five species occur in most estuaries, in order from the seawards end: *G. locusta*, *G. zaddachi* (vars. and typ.), *G. chevreuxi*, *G. duebeni*, *G. pulex*. *G. locusta* overlaps *G. zaddachi salinus* at the mouth, while *G. zaddachi* typ. overlaps *G. zaddachi salinus* at the one end and extends right up to overlap *G. pulex* in fresh water, where, however, it does not reproduce. Mr D. Lack, Capt. C. Diver, Mr C. S. Elton, Mr H. D. Thomas and Dr G. C. Varley took part in the discussion which followed.

Dr J. Rżoska discussed some pre-war work on the ecology of Polish lakes, concerned largely with the quantitative development and distribution of the littoral fauna in two widely separated lakes of different nutritional standards. The diverse population of the littoral zone and the vertical distribution of species were illustrated by records of density and biomass, the zoning of Oligochaetes providing detailed examples. In the 'Charactum' the fauna remains very stable, records for successive summers showing constant numerical relations among its major components. Study of the history of the invasion of one lake by *Drissensia polymorpha* in 1933 was unfortunately interrupted by the war. Mr C. S. Elton, Dr G. M. Spooner, Dr E. D. le Cren, and Capt. C. Diver raised questions.

Mr J. B. Cragg, discussing the blowfly fauna of carcasses with special reference to sheep blowflies, recorded that *Lucilia sericata* was by far the commonest species emerging from carcasses of sheep killed by blowfly myiasis, being replaced by increased yields of *L. caesar* and *Phormia terrae-novae* after deaths from other causes. *Calliphora vomitoria* and *C. erythrocephala* rarely occurred, although the latter invariably emerged along with *L. caesar* and *L. illustris* from carcasses of small mammals and birds. It was also shown that full-fed larvae of *Lucilia* and *Calliphora* migrate extensively away from the carcass (up to 27 ft., *Lucilia*) while *Phormia* pupates within the carcass and predaceous larvae rarely move more than a few feet away. The nature of the fauna is probably influenced by changes in temperature resulting from larval activity, which may exceed 45° C. in cases of death from myiasis. Mr L. Davies, Dr G. C. Varley, Mr C. S. Elton and Dr G. M. Spooner took part in discussion afterwards.

Dr G. C. L. Bertram's paper, on 'Some Aspects of Human Ecology', considered *Homo sapiens* from an objective point of view, and indicated that, despite his power of exerting pressure on the environment for purposes of food production, fuel, housing, transport and the like, nevertheless the population of the species has reached super-optimal numbers in some areas, owing to man's belief that individual death by competition is undesirable, and to the power of the species to continue reproduction at an almost undiminished rate despite the fact that some two-thirds of its numbers have insufficient food for full development. Few men have realized the supreme importance of relative rates of population accumulation, and it will be interesting to note whether in course of time the species will deliberately adjust its numbers to coincide approximately with an optimal density. Mr R. S. R. Fitter, Mr C. S. Elton, Mr T. G. Tutin, Prof. A. R. Clapham, Dr G. M. Spooner, Mr D. Lack, Mr B. D. W. Morley and Capt. C. Diver spoke on the issues raised by this paper.

The meeting then concluded after passing with acclamation a resolution thanking Mr Harvey and the Council of the University College of the South-west for their hospitality, and Miss Fisher, who returned from retirement to ensure the smooth working of the Hall of residence where visitors were accommodated.

## LONDON MEETING

15 MAY 1946

Held jointly with the Royal Meteorological Society on  
'Ecology and the Study of Climate'

On 15 May a joint meeting with the Royal Meteorological Society was held in the rooms of the Royal Society, in the absence of the President and Vice-Presidents, Dr H. Godwin taking the Chair. The President of the Royal Meteorological Society, Mr G. Manley, opened the discussion with a paper on 'Variations in the Length of the Frost-free Period'. He demonstrated the greater incidence of frost in a narrow valley situated so as to collect cold air and contrasted this with the situation on the slopes of the Malverns where the topography does not favour the collection of cold air. By comparison of two areas, one in the Breckland and one at Cambridge, he showed that differences in heat-capacity and conductivity of the soil might lead to substantially different frost duration. Within built-up areas frost incidence is naturally low. Mr Manley showed a frost-free period of about four and a half months for a low-lying Midland situation, and one of only two months in the Breckland. He examined also the secular trend of minimum temperatures through the last century and a half, concluding that December and January frosts have become somewhat less severe.

Mr W. R. Day of the Imperial Forestry Institute, Oxford, spoke on 'Local Climatic Effects on Tree Growth' referring to the two factors of frost and wind-exposure. The trees which suffer most in this country appear to have a seasonal habit of growth which is out of accord with the climatic cycle, beginning growth too early, or continuing it too long: the European larch and Corsican pine illustrate this. Other trees liable to damage are those which would normally occupy a late stage in the woodland succession and would, therefore, develop in protection of established cover, but which are now grown exposed in plantations. In this category he cited oak, ash, beech, spruce and Douglas fir. This latter group suffered severely in the years of 1927, 1935 and 1945 when frost injury was widespread and when either early spells of warmth

had induced premature growth, or when late frosts occurred after normal growth had begun. Mr Day showed how the density and cover of plantations altering throughout development causes at first increasing and then decreasing susceptibility to frost injury, and he demonstrated increase of damage with increasing altitude. Exposure to wind was difficult to estimate quantitatively but was much affected both by elevation and local topography: it caused diminished height-growth.

Prof. C. Brunt, President of the Physical Society, read a paper on 'Some Factors in Microclimatology'. He related microclimatic situations primarily to the absorption of solar radiation by day and to heat loss by long-wave radiation at night. Factors influencing the temperature of the soil surface and overlying air include moisture content, reflecting power, heat capacity and conductivity of the surface layers, and vapour pressure of the air. The temperature gradients for three contrasting vegetation types, an antirrhinum flower bed, a wheat field, and high forest, were considered. The level of the absorptive and radiating layers and the effectiveness of plant material in preventing air movement were both shown to be important factors in the situation.

Dr G. C. Evans read a paper by Dr P. W. Richards and himself on 'Climate within a Tropical Rain Forest'. The data were from Nigerian forest and showed the daily march of temperature, relative and absolute humidity and of saturation deficit. They showed a striking temperature inversion and a condition of maintained high humidity in the lower canopy. (Reference may be made to Dr Evans's paper 'Ecological studies on the rain forest of Southern Nigeria. II. The atmospheric environmental conditions' in vol. 27, p. 436 of this *Journal*.)

Dr A. S. Boughey gave an account of 'The Effect of Climate on the Distribution of Plant Diseases in the Sudan'. The results showed the correlation between the amount of annual precipitation and the occurrence of certain important diseases of crop plants. This correlation is high with diseases caused by bacteria, smuts and Fungi Imperfecti, and may permit forecasting and forestalling of damage. It may also strongly determine geographical limitations for the cultivation of particular crops.

An interesting general discussion closed the meeting, fuller accounts of which will be found published in Day, W. R., 'Ecology and the study of climate', *Nature, Lond.*, 157, 829, 22 June 1946; and in the report of the meeting in the *Quarterly Journal of the Royal Meteorological Society* for April 1946 (vol. 72).

## SUMMER MEETING AT SHEFFIELD

2-5 JULY 1946

At the kind invitation of Prof. Clapham, the first Summer Meeting of the Society since 1939 was held at Sheffield. The meeting opened with the assembly of about forty members together with many interested guests from the Sheffield district at a most friendly and successful soirée in Crewe Hall, Clarkhouse Road at 8.30 p.m. on 2 July.

Wednesday, 3 July

On the following morning the party travelled by car and bus to Cressbrook Dale and afterwards to Padley Woods. Immediately to the west of Sheffield at 1300 ft. altitude and on the Millstone Grit formation *Calluna-Vaccinium* moors were passed, with *Eriophorum vaginatum* on deeper peat in wetter situations, and much *Deschampsia flexuosa* and *Vaccinium vitis-idaea* along drainage channels. Grazed areas were marked by *Deschampsia flexuosa*, *Festuca ovina*, *Nardus stricta* and *Agrostis*. The burning and grazing associated with sheep and grouse culture superimposed on the edaphic factors made a mosaic of vegetation types very striking in its colouring. By way of Haycop Tor the party entered Cressbrook Dale which lies in the strongly contrasting district of the Carboniferous Limestone. The vegetation of the dale is clearly that of ancient woodland fragmented and suppressed by cutting and grazing. At the head of the dale the disforested slopes had been disturbed by lead-mining and stone-wall quarrying and on the debris occurred an interesting range of limestone scree plants. Surface decalcification on gentler slopes, possibly emphasized above chert bands, was indicated by such calcifuge species as *Galium saxatile*. On these grassy sides of the valley a very large number of species of flowering plants was encountered, including *Arenaria verna*, *Saxifraga hypnoides*, *Carex ornithopoda*, *C. pulicaris*, *C. panicea*, *C. flacca*, *C. caryophyllea*, *Aquilegia vulgaris*, *Thalictrum collinum*, *Alchemilla alpestris*, *A. minor*, *A. pratensis*, *Cirsium heterophyllum*, *Trollius europaeus*,



*Orchis fuchsii*, *Parnassia palustris*. Fragments of natural ash-wood lower down the valley contained scrub patches with *Cornus sanguinea*, *Sorbus aucuparia*, *Corylus avellana* (v.ab.), *Ligustrum vulgare*, *Euonymus europaeus*, *Crataegus*, *Viburnum opulus*, *Acer campestre*, *Ulmus glabra*, *Taxus baccata*, *Acer pseudoplatanus*, *Rhamnus cathartica*, *Prunus padus*, and *Salix atrocinerea*. By the stream *Alnus glutinosa* was abundant. Conspicuous in the undergrowth were *Geranium sanguineum*, *Campanula trachelium*, *Bromus ramosus*, *Hypericum hirsutum*, *Allium ursinum*, *Melica uniflora*, *Festuca gigantea*. On screes *Convallaria* was locally very abundant and persisting after wood clearance.

On the gently sloping top of Haycop Tor in a vegetation of abundant *Deschampsia flexuosa*, *Vaccinium myrtillus* and *Galium saxatile* a profile revealed about 2 in. undecayed plant remains, 1 in. decayed black humus,  $\frac{3}{4}$  in. grey leached top of the mineral soil, 2 ft. pale reddish loam with no limestone and occasional chert fragments; beneath this large lumps of limestone were present. Thus there are strong indications of incipient podsolization above the Mountain Limestone.

Very strong contrast with the Cressbrook Dale vegetation was evident in the woods next visited, i.e. Padley Wood in the Longshawe Estate and on Millstone Grit. Here the dominant trees are *Quercus sessiliflora* 25–30 ft. tall, with some *Sorbus aucuparia* and *Pyrus malus*, and a good deal of a species of birch which is verrucose and non-pubescent, but clearly not *Betula verrucosa*. There was abundant dense undergrowth of *Pteridium*, *Calluna*, *Vaccinium vitis-idaea* and *V. myrtillus*. Some sheep-grazing occurs and there are local grassy patches in the wood with *Holcus mollis*, *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Festuca ovina* and *Galium saxatile*.

In the evening at 8.0 p.m., a meeting was held in the Department of Botany in the University of Sheffield. The President was in the Chair and the following new members were elected: Dr S. Pradhan, Dr R. Scott-Russell, Mr M. T. Philipose, Dr W. S. Richards, Dr R. G. Newton, Dr G. Metcalfe, Dr A. J. Rutter, Miss M. S. Shaw, Mr T. L. C. Bottomley, Mr M. Ashby, Mr J. E. Turnbull, Mr M. E. Solomon.

Dr V. M. Conway then gave an extremely interesting address on 'The Vegetational History of the Southern Pennines'. She stressed the present aberrant status of cotton-grass moor, indicating that where this is now dominant the peat commonly shows abundant raised-bog sphagna throughout. Pollen diagrams from the raised bog at Ringinglow showed that peat formation began early in Zone VII of the zonation for England and Wales, and it seems likely that the high mountain peats began at the same time, although growth was very slow at first. Ringinglow showed deep *Sphagnum* peat with only a thin dirty skin of *Eriophorum* peat. From the bog at Bleaklow (altitude 2000 ft.) there is *Sphagnum* in the upper two-thirds of the profile, with very thick *Eriophorum* bands below this, possibly relating to climatic change at about 1200 B.C., also indicated by pollen and seeds of *Menyanthes*. Dr Conway was able to identify a recurrence surface, possibly correlated with Granlund's RY III in Sweden, and indicative of climatic deterioration at about 500 B.C. Above this there is a big fall in tree-pollen frequency, and at some date approximating to A.D. 1000 there is a great rise in the ratio of non-tree to tree pollen, an indication of widespread forest destruction. A very animated discussion followed, in which a large number of members took part.

#### Thursday, 4 July

In good weather an ascent was made of Kinderscout via Crowden Head. The approach was by poor siliceous grassland, *Agrostido-festucetum* with *Potentilla erecta*, *Galium saxatile* and *Carex binervis*. On a saddle at 1000 ft. was an eroded blanket-bog with dominant *Eriophorum vaginatum*, abundant *Vaccinium myrtillus*, some *Eriophorum angustifolium* and *Deschampsia flexuosa* in better-drained situations. This was fringed by *Nardus stricta* on the mineral soil or on shallow redistributed peat. The summit of Kinderscout itself is covered by a deeply dissected blanket-peat, and on the residual hags *Eriophorum vaginatum*, *Empetrum nigrum*, and *Eriophorum angustifolium* approximately share dominance, whilst *Rubus chamaemorus* is frequent. Some energetic digging permitted Dr Conway and Dr Godwin to demonstrate the following profile:

- 0–3 ft. Fresh *Sphagnum* peat, cymbifolia and acutifolia types, with some tendency to banding.
- 3–7 ft. A more decayed *Sphagnum-Eriophorum-Calluna* peat (cf. transition Zone VII–VIII).
- 7–8 ft. Abundant horizontal layers of *Eriophorum vaginatum*, overlying a tough, homogeneous, putty-coloured and highly decomposed peat with many beetle elytra and locally with *Molinia tussocks*.
- 8 ft. The blackened surface of the gritty mineral soil.

This profile is at an altitude of c. 2000 ft. in a region of about 65 in. yearly rainfall. The lower homogeneous peat certainly represents the initial waterlogging of the plateau as blanket-bog formation was initiated early in the so-called 'Atlantic' period.

On the return journey the party halted at Ringinglow where Dr Conway demonstrated some of the ecological features of this raised-bog. It exhibits a tendency to form a 'rand' with *Molinia*, and along the Burbage Brook is a grazed flush area with meadow grasses and abundant *Juncus effusus*. The western end of the bog is dominated by *Calluna* on drained peat with *Eriophorum vaginatum* subdominant. The top of the undrained bog is now dominated by *Eriophorum vaginatum*, but marginally besides *Calluna*, *Deschampsia flexuosa* and *Empetrum nigrum* occur; these reflect drying and are absent from the bog centre. A dug profile showed black, soot-impregnated *Eriophorum vaginatum* peat for the top 10 cm., but beneath this clean and fresh *Sphagnum-Eriophorum angustifolium* peat, very little humified. As relics from this former vegetation *Vaccinium oxycoccus* or *Erica tetralix* still exist in the present cotton-grass vegetation.

In the evening at 8.0 p.m. in the Botanical Department Mr J. G. Boswell gave an account of 'The Microbiology of some Acid Soils', a story of great interest and based upon research work directed by Mr Boswell in Sheffield. The investigated samples were from various vegetation types and generally far from industrial regions. The isolation and culture of bacteria and fungi from these soils was described, and reference was made to the extensive exhibits of material set out in the laboratory. Mr Boswell successfully attempted a general interpretation of the results in terms of the biochemical changes produced by the various organisms present, the gross changes they produce in the soil and the ways in which they reflect the drift of such changes. The main points established were the following: the total number of organisms in these acid soils is large, the fungi are represented by a limited number of forms, which, however, occur regularly, active sugar fermenters are present, some requiring fixed nitrogen, others capable of nitrogen fixation, no nitrogen fixation however occurs, cellulose decomposition is mainly due to fungi, protein decomposition is widespread and active, nitrifying bacteria are totally absent. Molecular degradation is general, oxidation by bacteria leads to the formation of organic acids and this gives high acidity, then the fungi germinate, grow fast and by breaking down the acids reduce acidity.

Mr Boswell's paper aroused great interest and many spoke in the discussion which followed. The President thanked the lecturer and Prof. Tansley, called on by the President, expressed the warm and sincere thanks of the Society to Prof. Clapham and his staff for the admirable arrangements of the meeting, to Dr Conway for her unstinted assistance as conductor and demonstrator and to the Crewe Hall authorities and staff for their kind helpfulness.

The meeting then adjourned for examination of the considerable series of ecological exhibits set out in the large laboratory: these included Mr Boswell's soil-organisms in culture; a demonstration by Mr J. Jackson of the decalcification of soil above Carboniferous Limestone and corresponding modification of flora; photographs of the vegetation of Trinidad by Mr N. G. Simmonds; pollen-diagrams, profiles and peat-samples from peat-bogs near Sheffield by Dr V. M. Conway, and data on atmospheric pollution in the Sheffield district also set out by Dr Conway. (At Dore, 4 miles west of Sheffield, there is an annual fall of 100 tons of solids per square mile, or about 1 oz. per square yard.)

#### Friday, 5 July

The party visited Anston Stones Wood which lies on Magnesian Limestone a few miles east of Sheffield. The limestone is very dolomitized and contains only about 3% of free carbonate. The wood lies on a steep valley slope broken part way down by small cliffs and ending in a river-flat with deeper soil at the bottom. The valley side is covered with mixed deciduous woodland with *Quercus robur*, *Fraxinus excelsior*, *Tilia platyphyllos*, *T. cordata*, *Ulmus glabra*, and *Sorbus aucuparia* in the tree-layer. *Taxus* and the limes were abundant on the cliffs, *Corylus* and *Ilex* were widespread and *Cornus sanguinea*, *Ligustrum vulgare*, *Viburnum opulus*, were frequent.

Mr H. G. Baker demonstrated interesting features in the autecology of *Melandrium rubrum* which was frequent in the wood, and Mr T. G. Tutin demonstrated some elements of the structure and behaviour of the bulbs of *Allium ursinum*. On abandoned agricultural soil on the far side of the valley dominated by *Brachypodium pinnatum* the party encountered the bee-orchis abundantly and discovered *Carex digitata*. Although the woodland showed signs of much planting Prof. Clapham suggested that evidence

of other woods supports the view that both species of *Tilia* are native on the Magnesian Limestone hereabouts.

The party returned in the early afternoon to catch trains from Sheffield, and so concluded a most successful recommencement of the Summer Meetings which our rules require us to hold each year, but which it was impossible to arrange during the war years.

H. GODWIN

## LONDON MEETING

15 OCTOBER 1946

By courtesy of the Council of the Royal Society a meeting was held on Tuesday, 15 October 1946, in the rooms of the Royal Society in Burlington House, for discussion of 'Survival and Extinction of Flora and Fauna in Glacial and Post-glacial Times: the Problem viewed in Relation to Quaternary Historical Investigations'. This meeting had been arranged by Dr H. Godwin in connexion with a working conference on Quaternary History and Pollen-analysis organized through the British Council, through whose generosity five distinguished workers from West-European allied countries had been enabled to attend.

The President, Dr A. S. Watt, introduced the foreign guests—Dr Knud Jessen, Professor of Botany in the University of Copenhagen; Prof. G. Dubois, Professor of Geology in the University of Strasbourg; Dr K. Faegri, Professor of Botany and Head of Bergen Museum, Norway; Dr J. Iversen of the Danish Geological Survey; and Dr F. Florschütz of Velp, Holland. Having indicated the scope of the subject and its considerable interest to British ecologists, Dr Watt called on Prof. Jessen to open the discussion.

Prof. JESSEN, speaking on 'The Temperate Irish Flora', recalled that the Society was met to discuss an ancient problem, one specifically treated by Dr Lloyd Praeger in his book published in 1932, and the central theme of the 1935 discussion held by the Royal Society. He stressed the need for facts in the form of discoveries of thermophilous plants in late-glacial or glacial deposits as a basis for theories of pre-glacial survival of our flora, and whilst unprepared to offer such facts he expressed and classified the problems involved. In the maximum glaciation the ocean shore lay far west of the British Isles, and at the latest glaciation, in which a good deal of England and Wales was not ice-covered, the sea was perhaps 100 m. below its present level. He suggested that in the Late-glacial development of Ireland, Zone III, the Late Dryas stage, corresponds with the formation of the great middle Fenno-Scandian moraines, and that, therefore, the preceding milder Allerød stage, Zone II, corresponds with the retreat of the ice across southern Sweden. He quoted the evidence of his own researches and of colleagues that in the Allerød stage there was tundra in northern Jutland, Park Tundra in middle Denmark, and open birch-pine woods in northern Germany. He showed that in Ireland the evidence pointed to tundra and Empetrum heath vegetation, the forest-belt correspondingly lying south of Ireland. If *Quercus sessiliflora* and *Arbutus unedo* existed on contiguous land to the south-west there must have been a very steep vegetational gradient to the *Salix herbacea* tundra of central Ireland.

A distribution map for Zone IV, the early post-glacial, in Ireland showed open *Salix herbacea* woodland with 75% of birch pollen, modest amounts of willow and a little pine pollen but no macroscopic remains of pine. *Ceratophyllum demersum* occurred in the van of thermophile invaders at Ralaghan. By pollen diagrams it was established that subsequent vegetational history in Ireland paralleled that in Denmark. The hazel began to spread in Zone V and reached immense values in Zone VI along with abundant pine, oak and elm. Leaves of *Erica cinerea* had been found in Zones V and VI, of *E. mackaii* in VI and VIIa, of *E. tetralix* in V, VI and VIIa, but all three were present in interglacial peat at Roundstone in Connemara, along with pollen of *Eriocaulon septangulare*, a plant of North American and western European distribution, which occurred in post-glacial times also in Zone VIIa. Nevertheless Prof. Jessen did not regard these facts as indicative of survival in place.

Dr J. IVERSEN speaking on 'Steppe Elements in the Danish Late-glacial Fauna' began by recalling Steenstrup's find from the shore of the Skager Rack, of the jaw of the ground-squirrel, *Spermophilus rufescens*. This, with other 'steppe' animals, such as the arctic hare, glutton, wild horse, bison, mouse hare, and giant Irish deer, had now been discovered in deposits of Late-glacial age. Numerous finds were cited, the bulk from the Late-glacial, and a few also from the immediately succeeding Pre-boreal and Boreal periods. The dating is based partly upon stratigraphy, but much more upon pollen-analysis of non-arboreal pollen, which shows the late-glacial vegetation in Denmark in Allerød times to have had an open 'park

tundra' character, of sedge and grass heath with scattered trees, chiefly birch. Forest existed in northern Germany, and there was nothing corresponding to 'steppe' therefore between the tundra and the Forest, nor was the fauna and flora purely 'Arctic', as is indicated *inter alia* by the abundance of pollen of *Artemisia* and of *Hippophae*. With amelioration of climate after the late-glacial the forest spread from the south and caused the extinction or withdrawal of the big mammals.

Prof. K. FAEGRI gave an account of changes in the past distribution of *Hippophae rhamnoides*, showing a map of its recent and fossil distribution in Fenno-Scandia. The fossil finds (late-glacial pollen) have a dense general distribution over central and southern Scandinavia. The present distribution is almost entirely linked to the coastline of the Baltic and parts of the Norwegian and west Swedish coasts, but there are also two isolated inland regions where steep cliffs carry a very open vegetation. It was suggested that the present-day restriction of range is not directly due to climatic causes, but that when forest closed in at the end of the late-glacial period competition from trees removed it from large areas. It is, furthermore, a somewhat calcicolous species and might be therefore taken, together with some other species, as effectively *aclimatic*.

Mr F. MITCHELL of Trinity College, Dublin, spoke of evidence of discoveries of the giant Irish deer (*Cervus megaceros*) and of the reindeer. A map of the distribution of the Newer Drift showed it not covering the Wicklow mountains or the Welsh mountains, and was used as the background geological picture for late-glacial events. A further map showed the numerous Irish sites where late-glacial stratigraphic sequences had been demonstrated and at nine of these *C. megaceros* had been found. These remains were chiefly in Zone II, the milder Allerød stage of open birch-willow vegetation with *Empetrum* heath in the west, a zone between the two colder phases of Zones I and III in which the vegetation was *Salix herbacea* tundra. A profile was shown displaying the giant Irish deer and reindeer in deposits of Zone II, overlaid by solifluction clays of Zone III containing Arctic plants such as *Oxyria digyna*, *Armeria* and *Dryas octopetala*. It was suggested that since Dr Farrington had shown this clay to correspond with the Wicklow Mountain glaciation, Zone III might be further correlated in Great Britain with the Scottish readvance.

A map of localities of reindeer discoveries was shown, some from limestone caves and others from open country, the latter very often with the giant Irish deer. The very numerous recorded finds of *Cervus megaceros* were also mapped and indicated a striking absence from the west and north-west regions of Ireland, the region where Prof. Jessen had shown the *Empetrum* heaths to prevail in Allerød times. It was apparent that large mammals flourished in the mild phase of the late-glacial and then were rapidly killed out, there being so far only one record suggesting survival of *Cervus megaceros* into the post-glacial period.

Dr K. B. BLACKBURN of Newcastle-on-Tyne spoke of discoveries of *Trapa natans* in the Outer Hebrides and *Alces alces* at Neasham, near Darlington. The *Trapa* nut was found by Prof. Heslop-Harrison floating in debris on the shore of a loch in South Uist off the west coast of Scotland, and from peat adhering to its surface a count of 140 tree-pollen was made. Comparison with a pollen-profile from a neighbouring site suggested an origin in the Atlantic period. The discovery represents an enormous western extension of the recorded range of the post-glacial fossil finds of this species. (For detailed account see *The New Phytologist*, vol. 45, p. 124, 1946.) The discovery of *Alces alces*, the moose, was made in a peaty band, between two clay layers in a brickpit at Neasham. Pollen analyses show the peat to have formed in a period of birch dominance with small amounts of pine and willow but with rather substantial amounts of hazel: it was tentatively suggested that the peat layer might represent the Allerød phase of the late-glacial period.

Prof. A. R. CLAPHAM read a paper by Prof. J. W. Heslop-Harrison (who was unable to be present), on 'The Bearing of Recent Investigations into the Flora and Fauna of the Inner and Outer Hebrides'.

The meeting was thrown open for general discussion. Prof. S. E. Hollingworth and Prof. F. E. Zeuner raised questions concerning geological and pedological conditions.

Mr A. J. Wilmott agreed with the necessity for facts before accepting the hypothesis of pre-glacial survival of the Irish Lusitanian plants, but pointed out how members of this flora in Ireland may now be hardier than is realized. He stressed the great differences between Atlantic and Continental climates, suggesting that this might have had great influence in the Glacial period and in late-glacial times.

Mr C. S. Elton, and Prof. S. E. Hollingworth also contributed to the discussion.

Prof. Jessen replying to Mr Wilmott pointed out that solifluction effects were general throughout Ireland, and asked whether *Arbutus* could be conceived to have remained under such conditions either in

its present station or on the continental shelf. He agreed that a lot of Boreal plants might have had chance of pre-glacial survival. With regard to the *Trapa* discovery he expressed doubts raised by the demands of the plant for high summer temperatures.

Dr J. B. Simpson spoke of the glaciology of the islands off the Scottish coast: Coll and Tiree were completely glaciated. He questioned whether enough weight had been given to the possibility of human introduction along the main Viking routes. Dr A. Farrington spoke of Mr Mitchell's reconstruction of the late-glacial ice distribution and asserted that the local glaciation of the Wicklow mountains is certainly later than the Newer Drift. Dr P. W. Richards suggested that the evidence of the British bryophytic flora is of particular value in this field of inquiry because of the large number of relict species. Some of the mosses concerned are not known to have any reproduction by sporophytes or spores. Dr K. P. Oakley, Dr F. Florschütz, Dr W. A. Clark also spoke in the discussion, which was terminated by the President at 5.0 p.m. About 70 or 80 members and guests were present at the meeting.

Published papers bearing directly upon the subjects of this discussion are:

- Faegri, K. (1935, 1939-40, 1943).** Quartärgeologische Untersuchungen im westlichen Norwegen. *Bergens Mus. Aarb.* Nr. 7-8.
- Heslop-Harrison, J. W. & Blackburn, K. B. (1946).** The occurrence of a nut of *Trapa natans* L. in the Outer Hebrides, with some account of the peat-bogs adjoining the loch in which the discovery was made. *New Phytol.* **45**, 124.
- Iversen, J. (1934).** Fund of Vildhest (*Equus caballus*) fra Overgangen mellem Sen-og Postglaciale tid i Danmark. *Danm. geol. Unders.* **4**, 13.
- Iversen, J. (1945).** The Bison in Denmark: a zoological and geological investigation of the finds in Danish Pleistocene deposits. *Danm. geol. Unders.* **2**, 73.
- Jessen, K. & Farrington, A. (1938).** The bogs at Ballybetagh, near Dublin with remarks on late-glacial conditions in Ireland. *Proc. R. Irish Acad.* **44**, B, 10.
- Mitchell, G. F. (1940).** Studies in Irish Quaternary deposits: some lacustrine deposits near Dunshaughlin, Co. Meath. *Proc. R. Irish Acad.* **46**, B, 2.
- Mitchell, G. F. (1941).** Studies in Irish Quaternary deposits. 2. Some lacustrine deposits near Ratoath, Co. Meath. 3. The reindeer in Ireland. *Proc. R. Irish Acad.* **46**, B, 13, 14.
- Schütrumpf, R. (1943).** Die pollenanalytische Untersuchung der Rentierjägerfundstätte Stellmoor. In **Rust, A.,** *Die alt- und mittelsteinzeitlichen Funde von Stellmoor.*
- Trechman, C. T. (1938).** A skeleton of elk (*Cervus alces*) from Neasham, near Darlington. *Proc. Yorks. Geol. (Polyt.) Soc.* **24**.

(It is hoped that the results of Prof. Jessen's very extensive Irish investigations will shortly be published in the *Proc. R. Irish Acad.*)

## ANNUAL GENERAL MEETING

SATURDAY, 11 JANUARY 1947

The Annual General Meeting of the Society was held in the Department of Botany, University College, London, on Saturday, 11 January 1947, the President, Dr A. S. Watt in the Chair and approximately 100 members present.

The minutes of the last Annual General Meeting were read and signed and apologies for absence were notified from Dr E. Wyllie Fenton, Prof. A. C. Hardy, Dr G. M. Spooner, Mr C. Diver, Mr I. Hepburn and Mr G. C. L. Bertram.

The report of the Hon. Secretaries on the work of the past year was read and accepted.

### *Report of the Hon. Secretaries for the year 1946*

The thirty-second Annual Meeting of the Society was held in the Washington Singer Laboratories of University College, Exeter, on Friday, 4 January 1946. The business meeting at 10 a.m. was followed by seven papers on various aspects of plant and animal ecology. Rather more than 60 members attended the meeting. A soirée and exhibit of ecological material formed part of the programme and there was a conducted visit to the famous arboretum in the University College grounds. The Society is much indebted to Mr Harvey and his colleagues for their organization of this most successful meeting and to the University College authorities for their hospitality.

On 15 May 1946, in the rooms of the Royal Society, a joint meeting was held with the Royal Meteorological Society at which were read a series of papers on the relation of ecology and the study of climate. The meeting was well attended and instructive both to meteorologists and to ecologists: it is apparent that there is scope for much closer cooperation between workers in these two fields of investigation.

For the first time since August 1939, it proved practicable to arrange a Summer Meeting with field excursions, and by the generosity of Prof. Clapham and the authorities of his University, this was held at Sheffield from 2-5 July. The party of about fifty were conducted to Cressbrook Dale, Kinder Scout, Padley Wood, Ringinglow and Anston Stones Wood, thus seeing vegetation types on Millstone Grit, Mountain Limestone and Magnesian Limestone. Most interesting evening talks were given by Dr Conway and Mr Boswell, and an exhibit of ecological material was also staged.

A second London meeting was held on 15 October to discuss 'Survival and Extinction of Flora and Fauna in Glacial and Post-glacial Times, as affected by the Evidence of Quaternary History and Pollen-analysis'. As guests there were present Prof. Knud Jessen of Copenhagen, Dr J. Iversen of the Danish Geological Survey, Prof. Knut Faegri of Bergen, Prof. G. Dubois of Strasbourg, Dr F. Florschütz of Velp, Holland, Mr Frank Mitchell of Trinity College, Dublin, and Dr A. Farrington, Secretary of the Royal Irish Academy. In a series of interesting papers our visitors showed that the vegetation and climate of the late-glacial and early post-glacial phases in these islands and in western Europe are now becoming clear, and that knowledge of fauna and flora of these periods is growing rapidly.

In the past year two numbers of *The Journal of Animal Ecology* have been published, appearing respectively in May and November; they contain respectively 122 and 90 pages. Seventeen original articles were published with 10 plates, in addition to notices and reviews. Notices of publications on Animal Ecology in this volume totalled 183.

Since the last annual meeting only one number of *The Journal of Ecology* has appeared, and this was Part 2 of vol. 33 issued in July 1946: the first number of vol. 34, delayed by printing difficulties, should appear early in 1947.

Since the last annual meeting the membership of the Society has risen from 458 to 502 members. 18 members have resigned or died, and 62 new members have been elected. Of the present membership 260 members receive *The Journal of Ecology* alone, 158 *The Journal of Animal Ecology*, 81 members receive both journals, and 3 neither. This is the first time in the history of the Society that a membership of 500 has been reached; through the war years, beginning with 1939 the yearly membership figures have been as follows: 1939, 363; 1940, 361; 1941, 335; 1942, 363; 1943, 378; 1944, 398; 1945, 420; 1946, 458; 1947, 502. We record with regret the death of Prof. F. E. Clements the doyen of American ecology. Members will be aware that at this Annual Meeting the Council is proposing the election to honorary life-membership of Prof. Tansley, who has for so long been the leader of British Ecology and has rendered such valuable service to the Society.

Publication of the Biological Flora continues satisfactorily with the appearance of accounts of *Gentiana pneumonanthe*, and *Allium vineale* is in the forthcoming number.

The check-list of British Vascular Plants, for use with the Flora has, thanks to the persistent labour of Prof. Clapham, been published. It is available as a separate issue, and will no doubt prove of great general value to British botanists.

The Society has maintained its concern with matters of nature conservation: through Dr Eustace Jones the ecological viewpoint was represented to the Departmental Committee appointed to consider the future of the New Forest, and through Mr Harvey and other officers and Council Members ecological interests have been represented at the inquiries and meetings held in relation to acquisition of Dartmoor and similar sites for practice grounds for the Services.

Since the preparation of the Society's 'Memorandum on the Establishment of an Aerial Unit for Scientific Work' in April 1945, we note with pleasure that there has been set up an 'Advisory Committee for Airborne Research Facilities', along the lines recommended.

H. GODWIN

L. A. HARVEY

Mr Summerhayes reported on the financial position of the Society. Whilst the audit had not yet taken place and *The Journal of Ecology* was delayed in appearance, it was impossible to make close estimates, nevertheless he expected a small surplus on the year's working. Subscriptions had reached a record high

total of £700, and sales of the two *Journals* to non-members were almost back to pre-war level. Expenses for meetings had naturally and satisfactorily risen with the greater frequency of meetings, and it was to be expected that the Biological Flora would be an important future item of expenditure. It was proposed by the President, seconded by Prof. Clapham and carried *nem. con.* that the three following grants be made: (i) a grant of £10 to the Freshwater Biological Association for the year 1947; (ii) a subscription of £10. 10s. to the Parliamentary and Scientific Committee for the year 1947; (iii) a payment of £10 for admission of the Society to Honorary Life Membership of the Yorkshire Naturalists' Trust.

Prof. Tansley having drawn attention to the rising costs of printing and having envisaged a possible need to raise the subscription and selling price of the *Journals*, Prof. Pearsall, editor of *The Journal of Ecology*, spoke of the position of that *Journal*. Publication is now some six months in arrears and it is the intention of the Council to attempt to get back to normal publication times by printing during the year the equivalent of three numbers of the *Journal*, a proceeding which will be easier because we have in hand several long papers which were difficult to produce in the war years.

Dr P. W. Richards proposed the reappointment of Messrs William Norman & Sons as auditors for the Society: this was seconded by Sir Edward Salisbury and carried unanimously.

The meeting proceeded to the election of officers and council members as follows:

*Hon. Secretaries*: H. GODWIN, L. A. HARVEY.

*Hon. Editor 'The Journal of Ecology'*: W. H. PEARSALL.

*Hon. Editor 'The Journal of Animal Ecology'*: C. ELTON.

*Ordinary Council Members*: A. C. HARDY, G. M. SPOONER, G. C. L. BERTRAM, R. E. HUGHES, T. G. TUTIN.

The President, in bringing forward the recommendation of the Council that Prof. A. G. Tansley, F.R.S., be elected an Honorary Life Member of the Society, spoke of the exceptional contribution which Prof. Tansley had made to the establishment of British Ecology and of this Society. The proposal was adopted with prolonged acclamation. Prof. Tansley, thanking the Society for this signal honour recalled the early history of the Society, saying that he had proposed the formation of the British Vegetation Committee in 1904, a body which in 1913 resolved itself into the British Ecological Society, but that this transformation was chiefly due to the initiative of the late Prof. C. E. Moss, who pursued with great activity the pioneer work in ecology performed by the brothers William and Robert Smith. After the 1914-18 war there had been a time of quiescence, followed by the present period of rapid increase. He wished the Society much future prosperity.

Dr P. W. Richards indicated that six more accounts for the Biological Flora are ready for press, and a further two hundred are promised. The three editors are making a revised and simplified schedule; they propose to aim at a publication of twenty to twenty-five accounts each year and will in general restrict the length of each account to some 4000 words of text (including tables), i.e. to about 6 pages of type together with not more than 2 pages of text-figures. Accounts of communities should be in condensed form and for areas of stated and restricted size. Dr Richards asked members to contribute to the Flora addenda and corrigenda, and recalled that good-quality photographs of the species described would be of considerable value, and might at some future time, be published.

Prof. Tansley spoke of the work of the Wild Life Conservation Special Committee of the National Parks Committee of the Ministry of Town and Country Planning. It was hoped that the reports of the National Parks Committee and of the Wild Life Conservation Special Committee would appear together in the spring.

No other business being brought forward, at 11.55 a.m. the President, Dr A. S. Watt, gave an extremely interesting and fundamental address upon 'Pattern and Process in the Plant Community'.

After the adjournment for lunch the meeting was resumed at 2.15 p.m. when Dr J. B. Simpson, of the Scottish Geological Survey, gave an account of the 'Scottish Tertiary Flora' based upon his own pollen identifications from sedimentary beds beneath and within lava beds in Argyllshire. He exhibited a series of remarkable lantern slides each showing an enlarged fossil grain and a corresponding grain of the present-day species most closely resembling it. Some 70 species of flowering plants and gymnosperms were represented in the two beds investigated, comprising 43 genera and 20 families. In the upper, inter-basaltic bed, gymnosperm pollen was abundant and included species of the genera, *Ginkgo*, *Pinus*, *Cedrus*, *Picea*, *Podocarpus*, *Cryptomeria*, *Glyptostrobus*, *Taxodium* and *Cunninghamia*: gymnosperms were not

found in the lower bed. Among the genera of flowering plants recognized were *Nelumbium*, *Corylus* (cf. *C. columna* and *C. ferox*), *Alnus* (cf. *A. cordata*, *A. japonica*, *A. sieboldiana*, *A. rubra* and *A. oregana*), *Planera*, many genera of the Proteaceae, *Casuarina*, *Eucalyptus*, and several genera of the Hamamelidaceae. Monocotyledon pollen was rare although *Aponogeton* had been identified. It was clearly brought out that this was a flora with very strong Australian, South African and Chinese affinities, whilst present-day European species were almost entirely absent.

In the discussion which followed Dr A. S. Watt, Dr H. Godwin, Prof. T. G. B. Osborn, Dr H. Hamshaw Thomas, Prof. A. R. Clapham and Dr G. C. Varley spoke, and the great interest and prospective expansion of such studies as Dr Simpson's were emphasized.

Dr C. B. Williams then spoke of 'The Logarithmic Series and the Problem of Intra-generic Competition'. It was demonstrated that the 'hollow curve' for numbers of genera with different numbers of species, both for animal and plant populations, fitted a hyperbolic curve badly, but fitted well a logarithmic series of the form  $ax$ ,  $\frac{1}{2}ax^2$ ,  $\frac{1}{3}ax^3$ , etc., where  $x$  is below 1. It was concluded that taxonomists had been driven insensibly to adopt an order turning out to be that of a logarithmic series, but that this being so it now should be possible to make use of the properties of the logarithmic series in deducing possibilities about population composition and to test them. Dr Williams passed from the analysis of faunas and floras of a country to those of successively smaller areas with a view to discovering whether there is evidence in the data of inter- or intra-generic competition. In the small areas the index of diversity is smaller than that of a random sample of the species, i.e. the species are less divided into genera. This would seem to show that competition exists rather between the genera than between the species of each genus. Corresponding with this it appears that the fact that one species has survived in a given locality makes it more likely that other species of the same genus will also survive. In the lively discussion which followed Major C. W. Hume, Mr A. C. Crundwell, Dr Pradhan, Dr T. A. W. Davies, Mr C. S. Elton, Mr K. R. Sporne, Mr D. B. Carlisle and Mr R. Ross took part; the difficulties of sampling populations with the arrangement of a logarithmic series were recognized and the validity of comparison of the various-sized units employed by Dr Williams was questioned.

Mr H. L. K. Whitehouse exhibited a beautiful aerial photograph of East Runton 'Common, Norfolk, taken at an altitude of 31,000 ft. a few days after the area had been visited by an ecological survey party. The photograph showed even the paths and quadrats made by the party and gave extremely valuable evidence supplementary to that collected on the ground.

Dr D. H. Valentine then gave his paper on 'Factors in the Isolation of Species' illustrating his thesis by referring to pairs of British flowering plants, and examining the nature of the various separating species and the ecological potentialities of any hybrid populations. Consideration was restricted to diploid species of the same chromosome number. The least degree of separation can be illustrated by *Plantago maritima*; where there are differences of habit and size there is total interfertility and isolation by ecological and geographical barriers so as to form ecotypes. A wider degree of separation is shown by *Melandrium dioicum* and *M. album* which are regarded with Baker as true species: they are ecologically separated by the respective woodland and cornfield habitat preferences, but are perfectly compatible and interfertile. Similar pairs are *Silene maritima* and *S. cucubalus*, and *Quercus robur* and *Q. sessiliflora* (= *Q. petraea*). The third stage, that of genetic isolation, is by incompatibility and reduced fertility added to geographical and ecological separation, as in *Primula acaulis* and *P. elatior*. Dr Valentine's own work shows that crosses with the primrose as female parent have seeds with a good deal less viability than those with oxlip as female parent and he suggested that the differing endosperm constitution might explain this. A similar situation appeared to exist in the cross between *Festuca pratensis* and *Lolium perenne*. The fourth degree of isolation is almost total incompatibility, as in the species *Primula veris* and *P. elatior*.

It would seem that in stage one there will be broad hybrid zones controlled by factors tending on one side to merge and on the other to separate the ecotypic populations. In the second stage when barriers are pronounced, hybrids form only at the rather unusual areas of contact. In the third stage contact of populations is restricted and the hybrid blocks are localized, and finally the species become separate and hybrids unknown, so that geographical and ecological barriers are unimportant and distribution areas may again overlap. Dr W. B. Turrill opened the discussion and quoted Dr Blakeslee's interesting discovery



that the development of hybrid plants of *Datura* could be greatly facilitated by extracting and growing the embryos on coconut milk. Dr H. G. Baker, Dr E. F. Warburg and Mr T. G. Tutin also contributed to the discussion.

At the conclusion of the meeting Dr O. W. Richards expressed the hearty thanks of the Society to our hosts, Prof. Pearsall and his colleagues of the Department of Botany, and thereto were added special thanks to the refectory staff for their admirable luncheon arrangements.

The Annual General Meeting had been preceded on the Friday evening by a very successful soirée in the Department at which the following ecological exhibits were displayed:

Miss E. E. A. Archibald. Vegetative Characteristics of some Chalkland Grasses.

Mr P. R. Bell. The Climate of the Carboniferous Age.

Mr A. B. Bradshaw and Mr R. L. Cuany. Variation in *Crataegus*.

Dr F. W. Jane and Mr R. Brinsden. Compression Wood in Conifers.

Dr F. W. Jane. Technique for the Identification of Charcoals.

Prof. W. H. Pearsall. British Sphagna.

Mr M. T. Phillipose. A Possible new species of *Chrysoamphitrema*.

Dr G. S. Puri. Litter in Woodlands.

Mr C. B. Rao. *Johannesbaptistia* and *Gloeotrichia*.

Miss J. Allison. Discovery of *Buxus* in a late Roman burial in Berkshire.

# LIST OF MEMBERS (13 JANUARY 1947)

E. = Takes *The Journal of Ecology*.

A. = Takes *The Journal of Animal Ecology*

Corrections, omissions or changes of address should be notified at once to the  
*Hon. Secretary*, Dr H. GODWIN, Botany School, Cambridge

- E. **Abery**, Miss W.; Provincial Education Office, Kampala, Uganda.
- E. **Abeywickrama**, B. A., B.Sc.; Botany School, Cambridge.
- E. **Ackroyd**, Miss B. I., B.Sc.; Soil Science Dept., School of Rural Economy, Oxford.
- E. A. **Adams**, Dr Charles C.; 149 Manning Boulevard, Albany 3, N.Y., U.S.A.
- E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
- E. A. **Airy Shaw**, H. K., B.A.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- A. **Alee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
- A. **Alexander**, W. B., M.A.; University Museum, Oxford.
- A. **Allen**, E. F., B.A., M.B.O.U.; Dept. of Agriculture, Teluk Anson, Perak, Malaya.
- E. **Allison**, Miss I. J., B.A.; Newnham College, Cambridge.
- E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dharma College, Lahore, India.
- E. **Andersonian Naturalists' Society** (cf. Glasgow).
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- E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
- E. **Ashby**, Prof. Eric, D.Sc.; Victoria University, Manchester.
- Ashby**, K. R., B.A.; Wray Castle, Ambleside, Westmorland (*Associate Member*).
- E. **Ashby**, Dr M.; 2 Redlands, Tiverton, Devon.
- E. **Asprey**, Dr G. F.; Botany Dept., The University, Aberdeen.
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- E. **Bakker**, Dr E. M. van Z.; Botanical Dept., University College, Bloemfontein, S. Africa.
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- A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
- E. **Barnes**, Mrs M., B.Sc.; East Fernbank, Kames Bay, Millport, Scotland.
- Barton**, Miss Frances M.; 19 Park Street, Bath (*Associate Member*).
- E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
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## THE LOGARITHMIC SERIES AND ITS APPLICATION TO BIOLOGICAL PROBLEMS

By C. B. WILLIAMS, Sc.D., *Rothamsted Experimental Station, Harpenden*

(With five Figures in the Text)

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### 1. INTRODUCTION

In the course of biological investigations of a numerical character the observer frequently obtains values which can be arranged in a discontinuous series of the type known as a 'frequency series'.

For example, there may be a random collection of a number of insects which have been classified into species. In this case the number of species with one individual, with two, with three individuals, and so on, would form a frequency series.

Alternatively, a collection might be made of a number of rats and on each the number of fleas counted. Then the number of rats with one flea, with two fleas, with three and so on, would again form a frequency series. Many other examples could be given, but most can be put under the general type of units classified into groups, or groups divided into units, which form a series of the numbers of groups with one, two or three, etc., units.

It is with one of the possible mathematical interpretations of such data—the logarithmic series—that we are concerned here. It was first suggested for biological problems by R. A. Fisher in 1943 (1), and a certain amount of information has already been published during the war; but owing to paper restrictions only a few reprints were obtained and the supply of them is already exhausted.

Dr R. A. Fisher has generously allowed me to quote freely from his contribution, so that all the relevant information can be collected together here.

Before discussing the mathematical properties of the series it must be pointed out that the data under consideration must be a randomized sample with no selection that would affect the size of the groups, or the number of groups of any one size. For example, a museum collection of butterflies in which every effort had been made to obtain many specimens of the 'rare' species, would not be suitable for consideration.

It is also important to understand that the original randomization of the sample may occur in two different ways, (1) by units and (2) by groups, as shown by the two examples given above.

## 254 *The logarithmic series and its application to biological problems*

In a randomized collection of individual insects (as, for example, a number of moths caught in a light trap) which are later classified into species, the catch is randomized on the individuals, and an addition to or an increase in the size of the sample will bring in new individuals to species already represented, i.e. new units in old groups.

If, on the other hand, collections of rats are made, and the number of fleas on each rat counted, then an increase in the number of rats examined will not add any fleas to the rats already counted, i.e. all the new units will be in new groups. In this case the sample is randomized by groups.

It will be shown below that samples taken from a population by these two different methods require different mathematical treatment.

### 2. THE LOGARITHMIC SERIES\* AND ITS PROPERTIES

In most elementary text-books of algebra there will be found the proof that

$$\log_e (1+x) = x - \frac{x^2}{2} + \frac{x^3}{3} - \frac{x^4}{4}, \dots, \text{etc.},$$

and the latter expansion is known as the 'logarithmic series'.

As negative terms have little or no meaning in biology, for our purpose it is better to write the equation

$$x + \frac{x^2}{2} + \frac{x^3}{3} + \frac{x^4}{4} + \dots = -\log_e (1-x), \quad (1)$$

or as a more general frequency series it can be written

$$n_1, \quad \frac{n_1 x}{2}, \quad \frac{n_1 x^2}{3}, \quad \frac{n_1 x^3}{4}, \dots,$$

where  $n_1$  is the number of groups with 1 unit, and the successive terms those with 2, 3, 4, etc., units.

The series is of course discontinuous and has an infinite number of terms.

#### *The total number of groups*

The sum of all terms to infinity, which is the total number of groups, is given by

$$S = \frac{n_1}{x} (-\log_e \overline{1-x}). \quad (2)$$

This is finite if  $x$  is less than unity; that is to say the series is then convergent.

The series therefore has two constants or parameters: ' $n_1$ ' which is the number of groups with one unit, and ' $x$ ' which is a number less than one.

The  $r+1$ th term is obtained from the  $r$ th by multiplying by  $rx/r+1$ , so the second term of the series is less than half the first, and the third term less than one-third of the first, and so on.

Two series of this form are shown in Table 1 and graphically in Fig. 1, A, and it will be seen from the figure that they form hollow curves of the same general appearance as a hyperbola. The nearer  $x$  approaches to unity the closer does the resemblance become; and in the limiting case when  $x=1$  the curve is identical with a harmonic series (hyperbola): the series is then divergent and the sum of its terms is infinite.

\* For the relation of the logarithmic series to the negative binomial see Fisher *et al.* (1943).

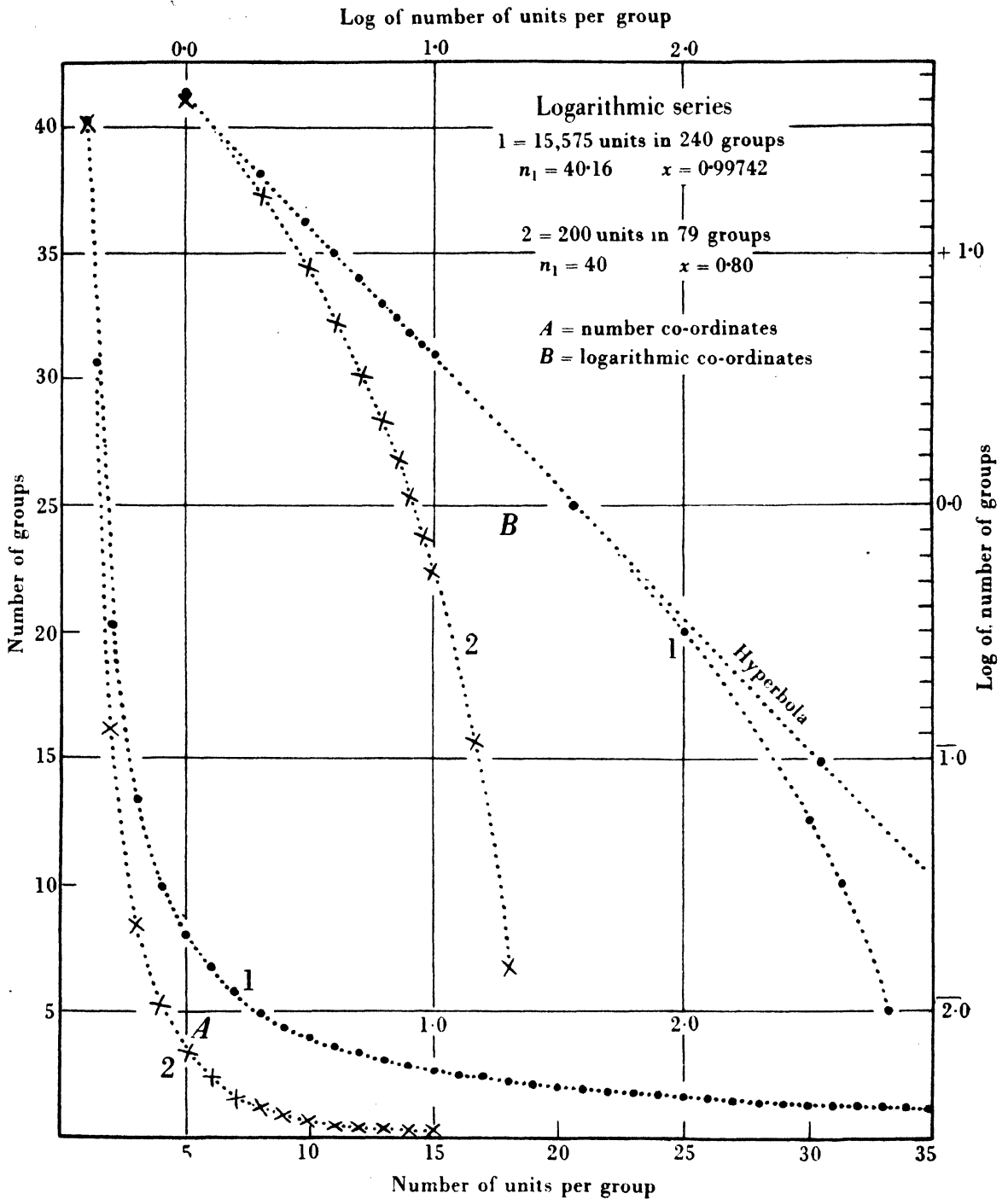


Fig. 1. Two examples of the logarithmic series from Table 1, plotted with number and with logarithmic co-ordinates.



*The total number of units*

Since the successive terms of the series are the number of groups containing 1, 2, 3, etc., units, it follows that the number of units in each successive term is

$$1n_1, \quad 2\frac{n_1x}{2}, \quad 3\frac{n_1x^2}{3}, \quad 4\frac{n_1x^3}{4}, \text{ etc.},$$

which equals

$$n_1, \quad n_1x, \quad n_1x^2, \quad n_1x^3, \text{ etc.}$$

Table 1. *Two examples of the logarithmic series*

	1	2	3
Term	15,575 units in 240 groups	200 units in 79 groups	Harmonic series* (hyperbola) for comparison
1	40.14	40.0	40.0
2	20.03	16.0	20.0
3	13.32	8.53	13.33
4	9.96	5.12	10.00
5	7.95	3.278	8.00
6	6.66	2.125	6.67
7	5.65	1.498	5.71
8	4.93	1.049	5.00
9	4.37	0.7460	4.44
10	3.92	0.537	4.00
20	1.92	0.02884	2.00
50	0.71	0.00001429	0.80
	$x=0.99742$	0.80	—
	$\alpha=40.24$	50.0	—

\* Number of groups and of units both infinite.

This is a geometric series, and its sum to infinity (i.e. the total number of units of the sample)\* is

$$N = \frac{n_1}{1-x}. \quad (3)$$

This is also finite if  $x$  is less than unity.

From (2) and (3) it follows that the average number of units per group equals

$$\frac{N}{S} = \frac{x}{(1-x)(-\log_e 1-x)}. \quad (4)$$

Thus for any average number of units per group there is only one possible value of  $x$ . When this has been calculated  $n_1$  can be obtained by multiplying  $N$  by  $(1-x)$ .

The relation between  $x$  and  $N/S$  is shown in Table 2 and graphically in Fig. 2.

Thus for any series of units classified into groups in the form of a logarithmic series, if the total number of units and the total number of groups are both known, it is possible to calculate  $x$  and  $n_1$ , and so the whole series. In other words, for any definite number of units and of groups only one logarithmic series is possible.

\* This is the same as the statistical expression 'first moment', which is the sum of the numbers of groups in each term multiplied by the number of units per group in that term.

The 'second moment', which is sometimes useful, is the sum of the number of groups in each term multiplied by the square of the number of units per group in that term, i.e. it equals

$$1^2n_1 + 2^2\frac{n_1x}{2} + 3^2\frac{n_1x^2}{3} + 4^2\frac{n_1x^3}{4}, \text{ etc.},$$

and this

$$= \frac{N}{1-x} \quad \text{or} \quad \frac{n_1}{(1-x)^2}.$$

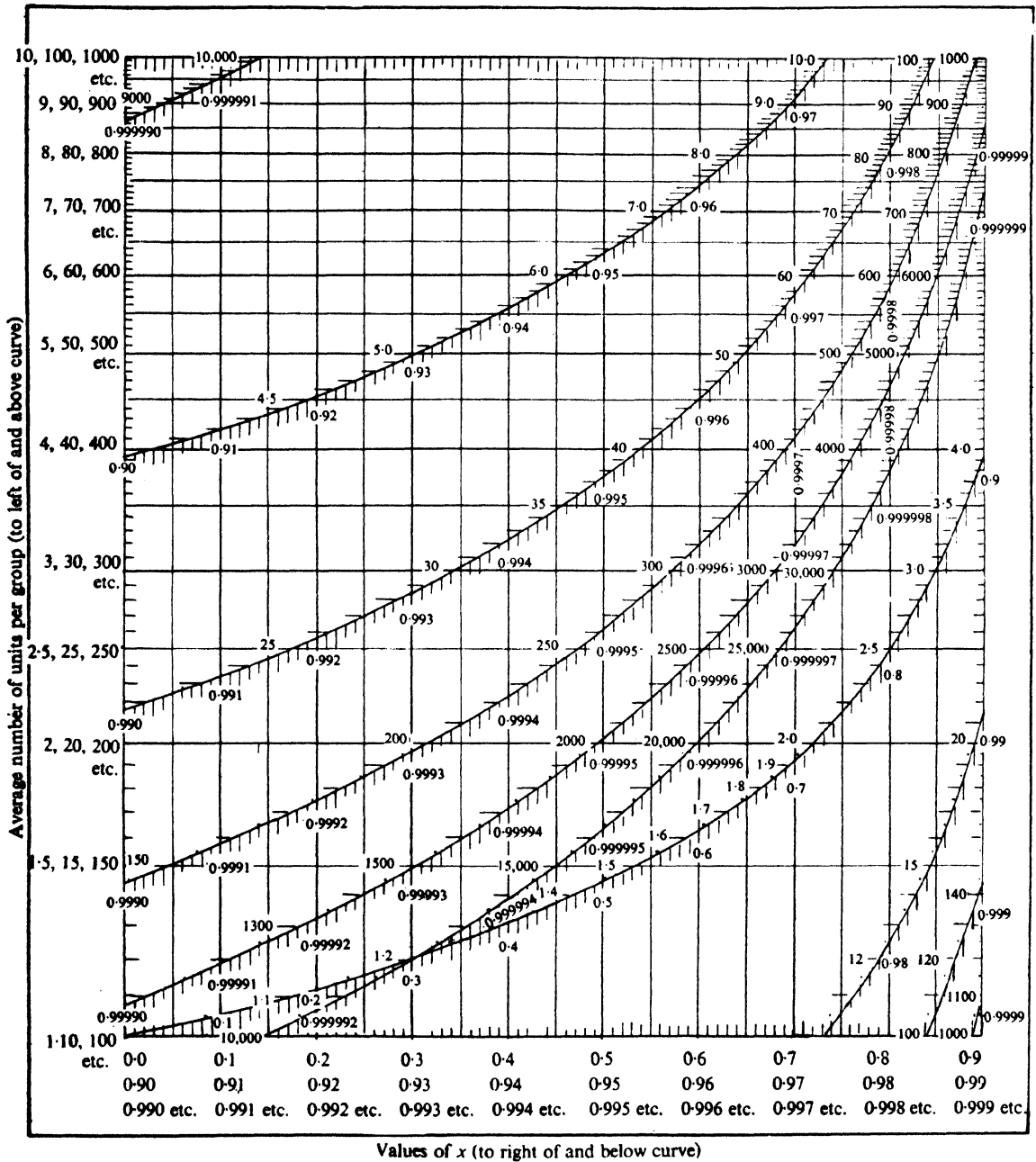


Fig. 2. The relation between the average number of units per group ( $N/S$ ) and  $x$  for all values of the former from 1 to 70,000. For any point on the ordinate there are several values in multiples of 10. The graph to be used for any value is indicated by the figures written immediately above the actual curve. Similarly the corresponding value of  $x$  to be used on the abscissa is indicated by figures written immediately along and below the actual curve.

Table 2. *Values of  $x$  with corresponding values of  $N/S$ , and  $n_1/S$* 

$x$	$N/S$	$n_1/S$	$x$	$N/S$	$n_1/S$
0.50	1.443	0.7215	0.992	25.68	0.2054
0.60	1.637	0.6548	0.993	28.58	0.2001
0.70	1.938	0.5814	0.994	32.38	0.1940
0.80	2.483	0.4966	0.995	37.48	0.1874
0.85	2.987	0.4480	0.996	45.11	0.1804
0.90	3.909	0.3909	0.997	57.21	0.1716
0.91	4.198	0.3778	0.998	80.33	0.1607
0.92	4.551	0.3641	0.9990	144.6	0.1446
0.93	4.995	0.3496	0.9992	175.1	0.1400
0.94	5.567	0.3340	0.9994	224.5	0.1347
0.95	6.340	0.3170	0.9996	319.4	0.1278
0.96	7.458	0.2983	0.9998	586.9	0.1174
0.97	9.214	0.2764	0.99990	1,086.0	0.1086
0.980	12.53	0.2506	0.99995	2,020	0.1010
0.985	15.63	0.2345	0.999990	8,696	0.0870
0.990	21.47	0.2147	0.999995	16,390	0.0820
0.991	23.38	0.2104	0.9999990	71,430	0.0714

*Transformation to logarithmic co-ordinates*

If a hyperbolic (harmonic) series of the form  $n_1, n_1/2, n_1/3$ , etc., is transformed graphically to logarithmic co-ordinates, both of numbers of groups and of numbers of units per group, it gives a straight-line relationship (Fig. 1, B). If a logarithmic series is so transformed (same figure) it gives a series of points on a line starting very near the hyperbola transformation but gradually departing from it more and more rapidly in a downward direction, i.e. giving fewer groups containing a large number of units than would be expected from the hyperbolic series. The nearer  $x$  is to unity, the longer the transformed series follows closely to the line of the hyperbola. This gives a rapid graphical method of testing if any set of figures is likely or not to represent a logarithmic series.

*Different samples from the same population*

If several samples of different sizes are taken by the same method from the same population, and if (see Introduction, pp. 253-4) the samples are randomized on units, then as the size of the sample increases the average number of units per group will also increase and hence  $x$  will increase.

As the size of the sample increases so also will  $n_1$ , the number of groups with one unit, increase; at first (with very small samples) rapidly, but more and more slowly as it approaches a limiting value.

*The index of diversity*

But for all samples taken from the same population by the same method the ratio of  $n_1/x$  is a constant,  $\alpha$ . That is,

$$\frac{n_1}{x} = \alpha \quad \text{or} \quad n_1 = \alpha x. \quad (5)$$

Since with increasing size of sample  $x$  gets nearer to unity but cannot exceed the value, it follows that the number of groups with one unit increases up to the limit of  $\alpha$ , but cannot exceed this, however large the sample may be.

The logarithmic series can therefore be written

$$\alpha x, \quad \alpha \frac{x^2}{2}, \quad \alpha \frac{x^3}{3}, \quad \alpha \frac{x^4}{4}, \quad (6)$$

which is sometimes a more convenient form.

In this case the total number of groups (e.g. species) is

$$S = \alpha (-\log_e \overline{1-x}), \quad (7)$$

and the total number of units (e.g. individuals) is

$$N = \alpha \frac{x}{1-x}. \quad (8)$$

Both  $n_1$  and  $x$  therefore vary with the size of the sample, but  $\alpha$  is constant for all samples (or summations of samples) from the same population taken by the same method of sampling. It is thus a property of the population sampled. It is high in populations which have a large number of groups relative to the number of individuals and low in populations which have a small number of groups relative to the number of units. We have called it the 'Index of Diversity', as it is a measure of the extent to which the units are associated into groups.

It follows from the above that

$$x = \frac{N}{N+\alpha} \quad \text{or} \quad \alpha = N \frac{(1-x)}{x}. \quad (9)$$

Thus if the total number of units and of groups is known in one sample from a given population, the index of diversity can be calculated; and from this it is possible to find the number of groups (and hence the frequency distribution) in any other sample, larger or smaller, from the same population.

The relation between the number of groups ( $S$ ), the number of units ( $N$ ), and the index of diversity is given by the formula

$$S = \alpha \log_e \left( 1 + \frac{N}{\alpha} \right). \quad (10)$$

Thus if  $\alpha$  is known for any population from any one sample it is only necessary to insert the new  $N$  for a second sample of a different number of units, in the above formula, to find the new  $S$  or number of groups.

For example, 15,575 moths were captured in a light trap at Harpenden and were found to belong to 240 species. This gives (see below)  $\alpha = 40.25$  approximately. From this we can calculate that had the sample contained only 1000 moths there would have been only about 130 species represented; if, on the other hand, one million moths could have been caught by the same method in the same time, about 405 species could have been expected.

Fig. 3 shows graphically the relation between the values of  $\alpha$  and the number of groups and units (e.g. species and individuals) in small samples up to 90 groups and 150 units. Fig. 4 (p. 265) shows larger samples up to 340 groups and 10,000 units. The units are plotted on a logarithmic scale. The relation between  $\log N$  and  $S$  is approximately linear for each value of  $\alpha$  for all large samples.

Fig. 5 (p. 268) shows a similar diagram for still larger samples up to  $S=900$  and  $N=10,000,000$ .

Table 3 shows some of the basic data from which these tables were prepared.

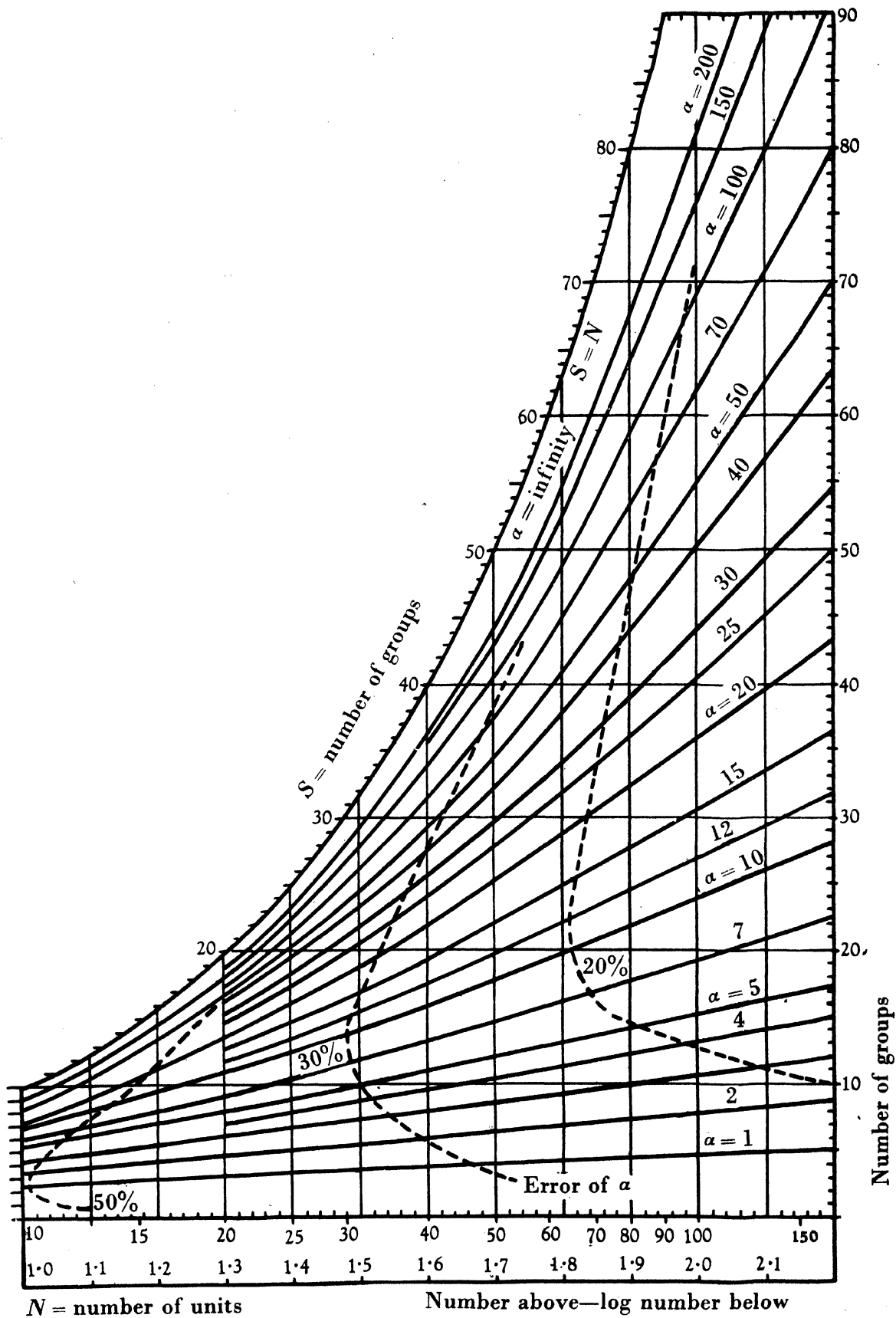


Fig. 3. The relation between  $S$ ,  $\alpha$  and  $N$  for values of  $N$  up to 150, and of  $S$  up to 90.

Of some biological interest are: (1) the average number of units per group (e.g. individuals per species); (2) the ratio of groups with one unit to the total groups (e.g. the proportion or percentage of monotypic genera); and (3) the proportion of the units which are found in groups of one unit only.

Table 3. *Values of S for different combinations of N and  $\alpha$* (From *J. Anim. Ecol.* **12**, 53.)

	N=10	20	50	100	200	500	1,000	2,000	5,000	10,000	100,000
$\alpha=1$	2.4	3.0	3.9	4.6	5.3	6.2	6.9	7.6	8.4	9.2	—
2	3.6	4.8	6.5	7.9	9.2	11.1	12.4	13.8	15.7	17.0	—
3	4.4	6.1	8.6	10.6	12.6	15.4	17.4	19.5	22.3	24.3	—
4	5.0	7.2	10.4	13.0	15.7	19.3	22.1	24.9	28.5	31.3	—
5	5.5	8.0	12.0	15.0	18.6	23.1	26.5	30.0	34.5	38.0	49.6
6	5.9	8.8	13.4	17.2	21.2	26.6	30.7	34.9	40.4	44.5	—
7	6.2	9.5	14.7	19.1	23.7	30.0	34.8	39.6	46.0	50.9	—
8	6.5	10.0	15.9	20.8	26.1	33.1	38.8	44.2	51.5	57.1	—
9	6.7	10.5	16.9	22.5	28.3	36.3	42.5	48.7	56.9	63.1	—
10	6.9	11.0	17.9	24.0	30.5	39.3	46.2	53.0	62.2	69.1	92.1
12	7.3	11.8	19.7	26.8	34.5	45.0	53.2	61.5	72.4	80.7	—
14	7.6	12.6	21.3	29.4	38.2	50.4	60.0	69.6	82.3	92.0	—
15	7.7	12.7	22.0	30.4	39.9	53.0	63.2	73.5	87.2	97.6	—
16	7.8	13.0	22.7	31.7	41.7	55.6	66.2	77.4	92.0	103.0	—
18	8.0	13.6	23.9	33.8	44.9	60.5	72.6	84.8	101.4	113.8	—
20	8.1	13.9	25.2	35.8	48.0	65.2	78.6	92.3	110.5	124.3	170.4
25	8.4	14.7	27.5	40.3	54.9	76.1	92.9	109.9	132.6	149.9	—
30	8.6	15.3	29.4	44.0	60.8	86.2	106.1	126.5	153.7	174.4	—
35	8.8	15.8	31.1	47.3	66.6	95.5	118.6	142.2	173.0	198.1	—
40	8.9	16.2	32.4	50.1	71.7	104.1	130.3	157.3	193.4	221.0	—
45	9.0	16.5	33.6	52.7	76.2	112.2	141.5	172.7	212.4	243.4	—
50	9.1	16.9	34.7	55.0	80.5	119.9	152.3	185.7	230.8	265.2	380.1
60	9.3	17.2	36.4	58.9	88.0	134.0	172.3	212.1	266.0	307.3	—
70	9.4	17.6	37.7	62.2	94.5	146.8	191.0	237.1	299.8	347.8	—
80	9.4	17.8	38.8	64.9	100.2	158.5	208.2	260.6	330.8	386.9	—
90	9.5	18.1	39.8	67.2	105.3	169.2	224.5	283.1	363.2	424.7	—
100	9.5	18.2	40.6	69.3	109.9	179.2	239.8	304.5	392.2	461.5	690.9
150	—	—	—	—	—	219.9	304.2	399.3	530.3	632.3	—
200	9.8	19.1	44.6	81.1	138.6	250.6	358.1	651.6	479.6	786.4	—

*The average number of units per group*

This is given by the formula

$$\frac{N}{S} = \frac{e^{S/\alpha} - 1}{e^{S/\alpha}} \quad \text{or} \quad = \frac{x}{(1-x)(-\log_e 1-x)}.$$

So for all samples with the same value of  $\alpha$  (i.e. from the same population) the average number of units per group is dependent on the size of  $S$ , or of  $x$ ; that is, on the size of the sample. It is larger with large samples and smaller with small samples (see Table 2 and Table 4, column 3, for examples).

*The proportion of groups with one unit*

This is  $n_1/S$  (or  $100n_1/S$  if expressed as a percentage), and is given by the formula

$$\frac{n_1}{S} = \frac{x}{-\log_e (1-x)}.$$

It is thus dependent on  $x$ , which is in turn dependent on the size of the sample for different samples from the same population (i.e. with the same  $\alpha$ ). It is large in small samples and small in large samples (see Table 2 and Table 4, column 6).

*The proportion of units in single groups to the total units*

This is  $n_1/N$  (or  $100n_1/N$  if expressed as a percentage), and is given by the formula

$$\frac{n_1}{N} = 1 - x.$$

This also varies with  $x$  and is large in small samples and very small in large samples from the same population. Examples of the different values of these ratios in different-sized samples from the same population are given in Table 4.

Table 4. *Numbers of species and other properties in different-sized samples from a population with an index of diversity = 100*

$N$	$S$	$N/S$	$x$	$n_1$	$100n_1/S$	$100n_1/N$
100,000	691	144.7	0.99902	98	14.2	0.098
10,000	461	21.7	0.9903	97	21.0	0.97
1,000	239	4.18	0.905	95	39.7	9.5
100	69	1.45	0.40	50	72.5	50
10	9.5	1.05	0.05	9.5	99.7	95

*The number and percentage of units in series of groups*

The number of units in the successive terms has been shown to be a geometric series

$$n_1, n_1x, n_1x^2, \text{ etc.},$$

and the sum to infinity  $N = n_1/(1-x)$ . The  $r+1$ th term is  $n_1x^r$ , and the sum of all the units from that term on to infinity is  $n_1x^r/(1-x)$ . So the total number of units in the first  $r$  terms inclusive is

$$\frac{n_1}{1-x} - \frac{n_1x^r}{1-x} = \frac{n_1}{1-x} (1-x^r).$$

The proportion of the total units that are in groups 1 to  $r$  is therefore

$$(1-x^r) \quad \text{or} \quad 100(1-x^r)\%.$$

For example, in a series with  $x=0.9$ , one-tenth of the units are in groups with one unit each, and 65.2% are in groups with 10 or less units per group.

If  $x=0.99$ , one-hundredth of the total number of units are in groups with one unit each, and 9.64% in groups with 10 or less.

Fifty per cent of the units are found in groups containing up to  $r$  units, where

$$r = \frac{\log 0.5}{\log x}.$$

Thus if  $x=0.9$ , 50% of the units are in groups with up to 6.6 units, i.e. up to between the sixth and seventh terms of the series.

If  $x=0.99$ , 50% of the units are in groups with 68 units or less.

Since for samples from the same population the value of  $x$  depends on the size of the sample, it follows that all the above proportions are dependent on the size of the sample.

But the proportions of units in groups of particular sizes is the same for all samples with the same  $x$ , and that is in all samples with the same average number of units per group.

It is not possible to get a simple expression for the proportion of *groups* in any series of terms of the logarithmic series.

*Sampling from a log series by units*

If a sample, randomized by units, is taken from a population arranged in a log series, the sample forms a new log series with the same  $\alpha$ , but with a different  $x$ . If the new sample contains a proportion  $p$  (i.e. 100 $p$ %) of the number of units in the population sampled, then the new  $x$

$$= \frac{px}{1 - (1-p)x}^*$$

For example, if one-third of the original population is taken in the sample the new  $x$

$$= \frac{0.33x}{1 - 0.67x}.$$

Since a sample of a population which is in a log series gives a log series in the sample, we are justified in assuming that, when we find a log series in a sample, the population sampled is itself in a log series.

*Sampling a log series by randomization of groups*

If successive samples of a population are based on randomization of groups (see Introduction, pp. 253-4) a different result is obtained. The successive samples have not, as above, the same  $\alpha$  and different values of  $x$ , but they have the same  $x$  and different values of  $\alpha$ .

For example, if a random sample of a rat population is taken and 50 rats are found infected with fleas, and on these are found 500 fleas, there will be an average of 10 fleas per rat with fleas. This gives  $x = 0.9732$  (approximately from Fig. 2) and  $\alpha = 14$  (approximately from Fig. 3). If now a second sample of similar size is taken, one would expect this also to have 50 rats and approximately 500 fleas. The two samples together (i.e. one larger sample) would thus have 100 rats and 1000 fleas, with  $x$  as before 0.9732, but  $\alpha = 28$  approximately.

*The error in estimate of  $\alpha$* 

Fisher has shown ((1), p. 56) that the standard error of  $\alpha$  is the square root of

$$\alpha^3 \frac{(N + \alpha)^2 \log_e (2N + \alpha/N + \alpha) - \alpha N}{(SN + S\alpha - N\alpha)^2}.$$

This is complicated to work out, but in Figs. 3 and 4 I have superimposed on the diagram lines of equal percentage error of  $\alpha$ . It will be seen that in general the error is high with small numbers of  $N$  and  $S$ . It is also high if  $S$  is large compared with  $N$  (a high value of  $\alpha$ ), or if  $N$  is very large compared with  $S$  (a low value of  $\alpha$ ).

Thus the error of estimation of  $\alpha$  is about 10% if  $N$  is 10,000 and  $S = 9$ ; or if  $N$  is about 250 and  $S$  from 50 to 100. The error is 30% with 30 individuals in 10 groups. With  $N = 10,000$  and  $S = 170$ , the error of  $\alpha$  is only about 3%.

Table 5 shows the standard error of  $\alpha$  for several different values of  $N$  and  $\alpha$ .

Table 5. *Error of  $\alpha$  for different values of  $N$  and  $\alpha$*

(From *J. Anim. Ecol.* 12, 53.)

	$N = 10$	100	1000	10,000	100,000
$\alpha = 1$	0.504	0.288	0.141	0.091	—
5	2.785	0.860	0.430	0.282	0.209
10	6.46	1.60	0.719	0.445	0.321
20	15.82	3.19	1.52	0.712	0.495
50	49.87	8.79	2.67	1.359	0.891
100	153.7	20.42	5.04	2.27	1.41

\* I am indebted to Mr M. H. Quenouille for this formula.



*The index of diversity and Yule's 'characteristic'*

I have shown (Williams (8)) that the index of diversity is proportional to the reciprocal of the 'Characteristic' defined by Yule in his *Statistical Study of a Literary Vocabulary* (Cambridge, 1944), which he used as a property of the population he was sampling. In his case this was the number of different nouns available for use in the mind of a writer.

Yule's characteristic =  $10,000 (S_2 - S_1)/S_1^2$ , where  $S_1$  and  $S_2$  are the first and second moments of the series. The index of diversity for the log series =  $S_1^2/(S_2 - S_1)$ ; but values calculated by this method are much more variable from sample to sample from the same population than values calculated by the methods given below.

## 3. METHODS OF FITTING A LOGARITHMIC SERIES TO KNOWN DATA

Two rapid preliminary steps may be taken to see if a logarithmic series is a likely explanation for any set of frequencies.

First by inspection of the numbers it should be checked that the second term should be less than half the first (within limits of error); the third term should be less than one-third of the first, etc.—and there should be a more or less steady fall.

A second rapid test is to plot the successive terms on a logarithmic scale (or on double log paper) and see if they approximate to the transformation shown in Fig. 1, at first near the straight line of the hyperbola and then falling away steadily and more rapidly.

If the total number of units and the total number of groups is known, the logarithmic series can be calculated by several methods varying in accuracy.

*Approximate method*

Calculate the average number of units per group ( $N/S$ ), and find  $x$  by inspection from Fig. 2, which shows the corresponding values of  $x$  for all values of  $N/S$  from 1 to 70,000.

*Example.* 15,575 moths caught in a light trap at Rothamsted were found to belong to 240 species. What is the corresponding logarithmic series?

The average number of individuals per species is 64.9. By inspection (Fig. 2),  $x = 0.9974$  approximately.

Hence  $n_1 = (1 - x) N = 0.0026 \times 15,575 = 40.5$ .

The series is therefore

$$40.5, \quad \frac{40.5}{2} \times 0.9974, \quad \frac{40.5}{3} \times 0.9974^2, \text{ etc.}$$

(For calculating the successive terms see below, p. 267.)

*Another approximate method*

If  $N$  and  $S$  are known an approximate value of  $\alpha$  can be read off from Figs. 3, 4 or 5.

*Example.* With the same data as above an inspection of Fig. 4 gives  $\alpha =$  approximately 40. Then

$$x = \frac{N}{N + \alpha} = \frac{15,575}{15,575 + 40} = 0.9974.$$

*A more accurate method* is based on Table 6 (first published by R. A. Fisher in *J. Anim. Ecol.* **12**, 55). The value of  $\log N/S$  is calculated, and the corresponding value of  $\log N/\alpha$  is found by interpolation in Table 5. Since  $N$  is known,  $\alpha$  can then be calculated.

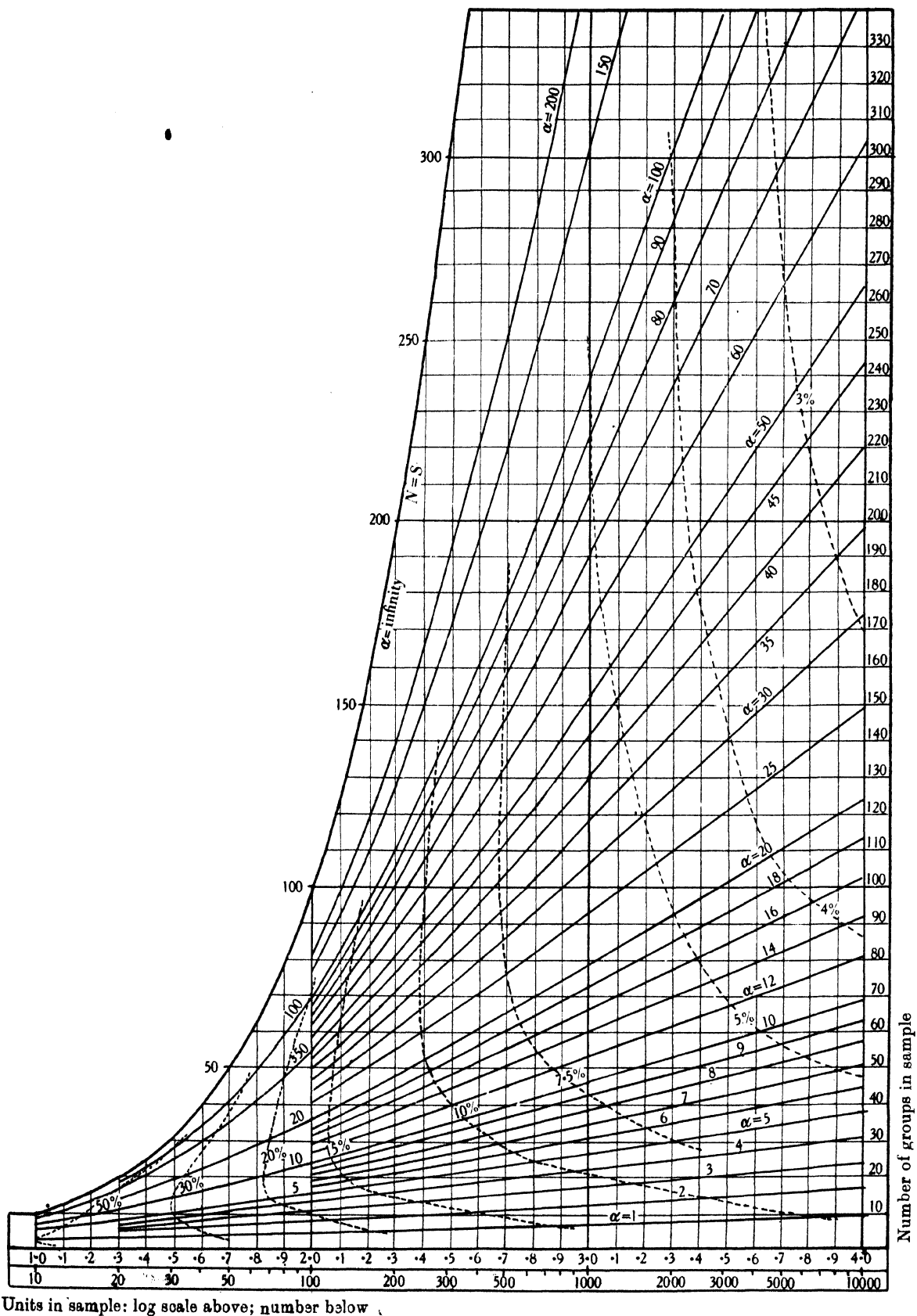


Fig. 4. The relation between  $S$ ,  $\log N$ , and  $\alpha$  for values of  $N$  up to 10,000 and of  $S$  up to 340.  
(From *J. Anim. Ecol.* 12, 52.)

## 266 *The logarithmic series and its application to biological problems*

*Example.* Data as above,  $N=15,575$ ,  $S=240$ :

$$\log N = 4.19243, \quad \log S = 2.38021.$$

Therefore

$$\log N/S = 1.81222.$$

From Table 6 it will be seen that:

$$\text{If } \log N/S = 1.82, \quad \text{then } \log N/\alpha = 2.59684.$$

$$\text{If } \log N/S = 1.81, \quad \text{then } \log N/\alpha = 2.58484. \quad (a)$$

Therefore the difference in  $\log N/\alpha$  for 0.01 difference in  $\log N/S = 0.01200$ . Since the relation over short distances is approximately linear the difference in  $\log N/\alpha$  for 0.00222 in  $\log N/S$  is 0.00266.

Adding this to (a) we get:

$$\text{If } \log N/S = 1.81222, \quad \text{then } \log N/\alpha = 2.58750,$$

but

$$\log N = 4.19243,$$

therefore

$$\log \alpha = 1.60492,$$

or

$$\alpha = 40.2644.$$

$$\text{Hence } x = \frac{N}{N + \alpha} = 0.9974214 \quad \text{and} \quad n_1 = 40.1617.$$

Table 6. *Values of  $\log N/\alpha$  for different values of  $\log N/S$  for solving equation  $S = \alpha \log_e (1 - N/\alpha)$ , given  $S$  and  $N$*

(From *J. Anim. Ecol.* 12, 55.)

$\log_{10} N/S$	0	1	2	3	4	5	6	7	8	9
0.4	0.61121	63084	65023	66939	68832	70701	72551	74382	76195	77990
0.5	0.79766	81526	83271	85002	86717	88417	90105	91779	93442	95092
0.6	0.96730	98356	99973	1.01579	03174	04759	06335	07902	09460	11010
0.7	1.12550	14220	15813	17331	18772	20136	21631	23120	24602	26077
0.8	1.27546	29008	30465	31916	33361	34801	36234	37663	39087	40506
0.9	1.41920	43329	44733	46133	47528	48919	50305	51688	53066	54440
1.0	1.55810	57177	58539	59898	61254	62605	63954	65299	66640	67979
1.1	1.69314	70646	71975	73301	74623	75943	77261	78575	79886	81195
1.2	1.82501	83805	85106	86404	87700	88994	90285	91574	92860	94144
1.3	1.95426	96706	97984	99259	2.00532	01804	03073	04340	05605	06869
1.4	2.08130	09389	10647	11902	13156	14409	15659	16908	18155	19400
1.5	2.20644	21886	23126	24365	25602	26838	28072	29305	30536	31766
1.6	2.32994	34221	35446	36670	37893	39114	40334	41553	42770	43986
1.7	2.45201	46414	47627	48838	50048	51256	52464	53670	54875	56079
1.8	2.57282	58484	59684	60884	62083	63280	64476	65672	66866	68059
1.9	2.69252	70443	71633	72822	74011	75198	76385	77570	78755	79939
2.0	2.81121	82303	83484	84664	85843	87022	88199	89376	90552	91727
2.1	2.92901	94075	95247	96419	97590	98760	99930	3.01099	02267	03434
2.2	3.04600	05766	06931	08095	09259	10422	11584	12745	13906	15066
2.3	3.16225	17384	18542	19699	20856	22012	23168	24323	25477	26630
2.4	3.27783	28936	30087	31238	32389	33539	34688	35837	36985	38133
2.5	3.39280	40426	41572	42717	43862	45006	46150	47293	48436	49578
2.6	3.50719	51860	53001	54141	55280	56419	57558	58696	59833	60970
2.7	3.62106	63242	64378	65513	66648	67782	68915	70048	71181	72313
2.8	3.73445	74577	75707	76838	77968	79097	80227	81355	82484	83611
2.9	3.84739	85866	86992	88119	89244	90370	91495	92619	93743	94867
3.0	3.95991	97114	98236	99358	4.00480	01602	02723	03843	04964	06084
3.1	4.07203	08322	09441	10560	11678	12795	13913	15030	16147	17263
3.2	4.18379	16494	20610	21725	22839	23954	25068	26181	27295	28408
3.3	4.29520	30632	31744	32856	33967	35079	36189	37300	38410	39520
3.4	4.40629	41738	42847	43956	45064	46172	47280	48387	49494	50601
3.5	4.51707	52814	53920	55025	56131	57236	58340	59445	60549	61653

An accurate method by trial and error is as follows. In this successive approximations are made to the value of  $x$ , and the result tested against the data.

*Example.* Data as above,  $N=15,575$ ,  $S=240$ . We know that

$$\frac{S}{N} = \frac{1-x}{x} (-\log_e \overline{1-x}).$$

If we use logs to the base 10 we get

$$\frac{1-x}{x} (-\log \overline{1-x}) = \frac{1}{2.30258} \times \frac{N}{S} = (\text{in this case}) 0.0066922.$$

We require to find a value of  $x$  that will fit this equation. Starting with a first approximation (from Fig. 2) of  $x=0.9974$ , we proceed as follows:

If $x$ equals	then $1-x$ equals	then $-\log(1-x)$ equals	$\frac{1-x}{x}$ then $(-\log \overline{1-x})$ equals	Conclusion
First approximation				
0.9974	0.0026	$-\bar{3}.4150$ $=2.5850$	0.006738	Too large; so make $x$ larger
Second approximation				
0.99742	0.00258	$-\bar{3}.4116$ $=2.5884$	0.006695	Slightly too large
Third approximation				
0.997421	0.002579	$-\bar{3}.4114$ $=2.5886$	0.0066932	Very slightly too large

and so on until the required accuracy is reached. The final value taken for  $x$  was 0.9974214.

Hence

$$n_1 = 15,575 \times 0.0025786 = 40.1617,$$

and

$$\alpha = N \frac{1-x}{x} = 40.2644.$$

*To calculate the series, or any one term*

This may be done by direct calculation on a calculating machine, but without this the simplest method is to use logs, and in this case the logs of reciprocals, given in most mathematical tables, are helpful.

The log of the  $r$ th term  $= \log n_1 + (r-1) \log x + \log 1/r$ . Since  $\log x$  is negative its value is subtracted from  $\log n_1$  in successive repetitions, and the log of the reciprocal added for each term.

*Example.* Data as above:

$$n_1 = 40.2644, \quad x = 0.9974214;$$

$$\log n_1 = 1.604917, \quad \log x = \bar{1}.998787 = -0.001213;$$

Term	$\log n_1 + (r-1) \log x$	$\log 1/r$	Total log	Number
1	1.604917	—	—	40.2644
2	1.603704	+	$\bar{1}.6990 = 1.3027$	20.08
3	1.602491	+	$\bar{1}.5229 = 1.1254$	13.35
4	1.601278	+	$\bar{1}.3797 = 0.9800$	9.550
5	1.600065	+	$\bar{1}.3010 = 0.9011$	7.963

and so on. For the 50th term

50	1.604917	$\log 1/50$	—	—
	$-(49 \times 0.001213)$	=		
	= 1.54448	2.3010	$\bar{1}.8455$	0.7005

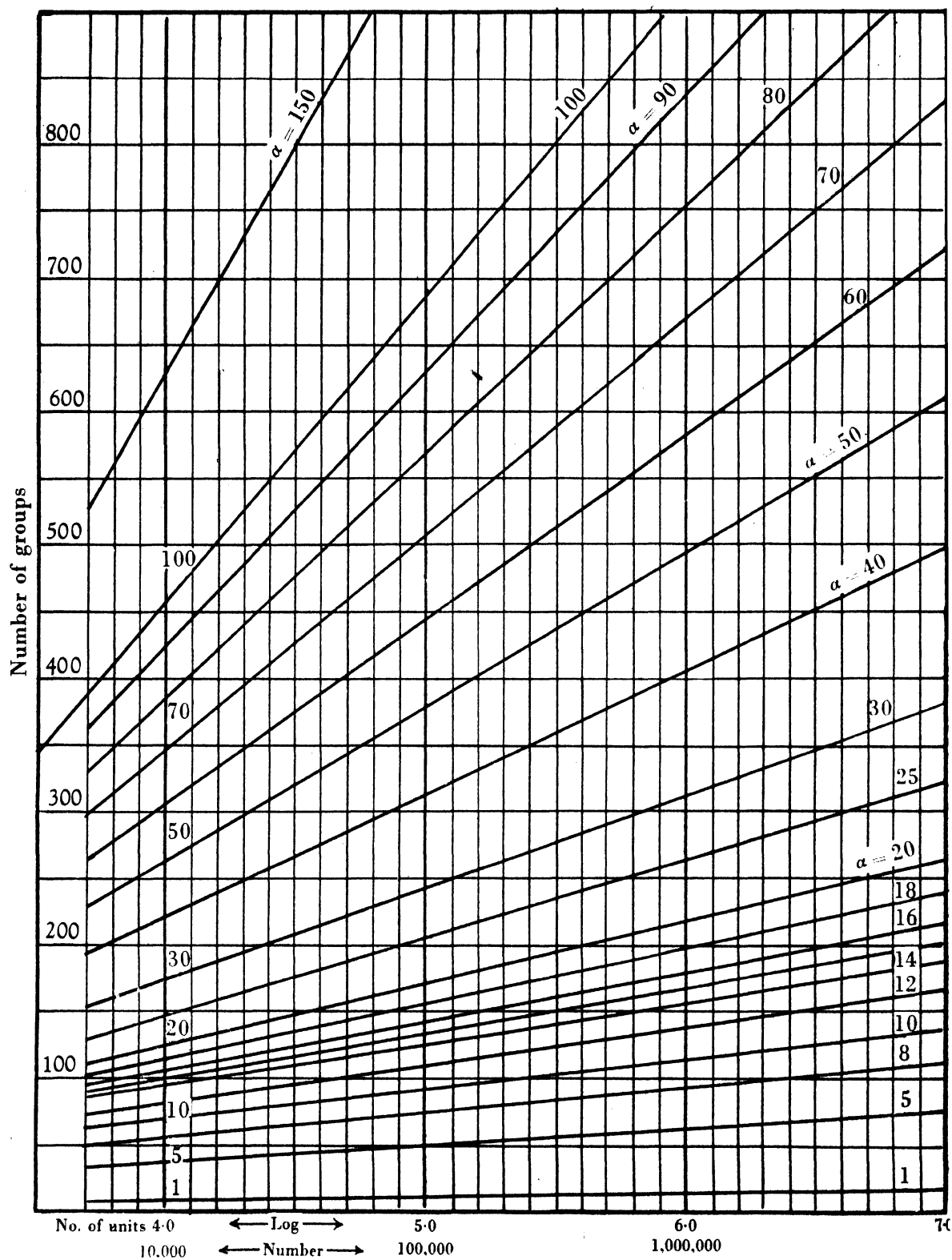


Fig. 5. The relation between  $S$ ,  $\log N$ , and  $\alpha$  for values of  $N$  from 10,000 to 10,000,000, and  $S$  up to 900.

*Alternate approximate method of finding the index of diversity  
from two samples of different sizes*

An approximate value of the index of diversity may be calculated for a given population, if two or more samples can be obtained of different sizes, neither small.

This method is particularly useful for botanical purposes, as, if the ratio between the different sample sizes is known, the actual number of individuals in each need not be counted. This makes it possible to find  $\alpha$  from the number of species of plants on two areas of different size, provided that we can assume, without serious error, that the number of individuals is proportional to the area of the samples. The actual numbers of individuals, however, must be large.

The method is based on the relation

$$S = \log_e \left( 1 + \frac{N}{\alpha} \right).$$

When  $N$  is very large compared with  $\alpha$  we can neglect the 1 in comparison with  $N/\alpha$  and say that

$$S \text{ is proportional to } (\log_e N/\alpha).$$

Hence, if two samples from the same population contain  $N$  and  $pN$  units,

$$S_{pN} - S_N = \left( \log_e \frac{pN}{\alpha} - \log_e \frac{N}{\alpha} \right) = \alpha \log_e p.$$

Thus if a sample size is multiplied by  $p$ , the number of groups (e.g. species) is increased by  $\alpha \log_e p$ .

If the size of a sample is doubled the number of species added is  $\alpha \log_e 2 = 0.693\alpha$ . If the size is multiplied by  $e$  ( $=2.718$ ) the number of species added equals  $\alpha$ . This latter fact could be easily applied to botanical surveys by using two quadrats whose diameters were in the ratio of 100 to 165 ( $=\sqrt{2.718}$ ). Then the average increase of species between samples of the two sizes would be a direct measure of the index of diversity. The samples must, however, be large enough to be representative even of the larger plants (see Jones & Williams (3)).

*Example.* Blackman (*Ann. Bot., Lond.*, 49, 760) states that the number of species of plants found on quadrats of various sizes in a grassland area in England was as follows:

Area in sq.in.	Average no. of species	Increase in no. of species on doubling size of sample
16	11.1	2.5
32	13.6	2.5
64	16.1	2.5
128	18.2	2.1
	Average	2.37

Therefore  $\alpha = 2.37 \div \log_e 2 = 2.37 \div 0.693 = 3.42$  approximately.

This is probably an underestimate as the samples are small, but as  $\alpha$  is also small the error will be relatively less.

*Calculation of the number of groups common to two samples*

An extension of the above method gives a means of finding the number of groups common to two large samples from the same population on the assumption that it conforms to the logarithmic series (for example, the number of species common to two areas of an ecological association). The samples, or areas must, however, be of different sizes.

## 270 *The logarithmic series and its application to biological problems*

Let the two areas be of size  $A$  and  $B$ , and the number of species in each  $a$  and  $b$ . If they are from the same population they will have the same  $\alpha$ , and if the samples are large we can neglect the 1 in comparison with  $N/\alpha$  in the equation  $S = \alpha \log_e (1 + N/\alpha)$ .

Let  $T$  be the total number of species in the two samples, then the increase in species by adding  $B$  to  $A$

$$= T - a = \alpha \log_e \frac{A+B}{A}.$$

The increase in species by adding  $A$  to  $B$

$$= T - b = \alpha \log_e \frac{A+B}{B}.$$

From these two equations  $T$  (and  $\alpha$ ) can be found and the number of species expected to be common to both  $= a + b - T$ .

*Example.* The island of Guernsey has 804 species of flowering plants on 24 sq. miles.

The island of Alderney has 519 species of flowering plants on 3 sq. miles.

On the assumption of identity of origin,

$$T - 804 = \alpha \log_e 1.125, \quad T - 519 = \alpha \log_e 9.00.$$

Hence  $T = 820$  and the number common to the two would be 503. The actual number observed was 480 which shows a high degree of relationship. For fuller discussion, see Williams ((6), p. 42), and Williams (9).

### 4. SUMMARY OF BIOLOGICAL APPLICATIONS OF THE LOGARITHMIC SERIES

The series has so far given reasonably good calculated fits to observed data in the following biological problems. The references are to the bibliography on p. 271.

#### A. *Individuals classified into species:*

- (1) Lepidoptera caught in a light trap at Harpenden, England ((1), pp. 44–8).
- (2) Capsidae caught in a light trap at Harpenden, England ((1), p. 49).
- (3) A collection of butterflies made in Malaya by A. S. Corbet ((1), p. 42 and (6), p. 15).
- (4) Butterflies from Mentawi Island, and from Karakorum ((1), p. 43).
- (5) Butterflies from Tioman Island, Malaya ((1), p. 43).
- (6) Elmidae (Coleoptera) from Mexico ((1), p. 43).
- (7) General population of British nesting birds ((6), p. 13).
- (8) Lepidoptera in light traps in U.S.A. (7).
- (9) Mosquitoes in light traps in U.S.A. ((6), p. 14).
- (10) Aphis caught on sticky traps in Derbyshire (Broadbent, data in *Proc. R. Ent. Soc.* ((21), pp. 41–6).
- (11) Spiders caught in nets (data Freeman, *J. Anim. Ecol.* 15, 70).

#### B. *Species and area (especially with plants):*

- (1) Grass land in Britain ((6), p. 3).
- (2) Aspen association in Michigan, U.S.A. ((6), p. 5).
- (3) Ground vegetation in Tectona forest, Java ((6), p. 9).
- (4) Species of plants common to related small areas, e.g. Channel Islands ((6), p. 42), São Tomé and neighbouring islands (9).
- (5) General discussion on area and number of species of plants (4).

C. *Parasites and host:*

- (1) Lice on heads of human beings ((6), p. 11).
- (2) Fleas on rats (unpublished data from J. L. Harrison).

D. *Species classified into genera:*

- (1) Orthoptera of world. Mantidae and Acridiidae ((6), p. 17).
- (2) Dermaptera of world ((6), p. 18).
- (3) Coccidae of world ((6), p. 18).
- (4) British Coleoptera ((6), p. 24).
- (5) British Lepidoptera ((6), p. 24).
- (6) British Cicadina ((6), p. 28).
- (7) British birds ((6), p. 29).
- (8) Flowering plants of the world ((6), p. 38).
- (9) British flowering plants ((6), p. 32).
- (10) British Capsidae (Miridae) (data from China, Ent. Soc. London. Generic names, Brit. Inst. Pt. 8).
- (11) Animals and plants in Ecological Communities (10).

F. *Miscellaneous applications:*

- (1) Number of publications by biologists (5).
- (2) Number of insects caught in nets at sea (unpublished data from A. C. Hardy).
- (3) Species of insects infesting food dumps (2).
- (4) Number of bacteria in colonies (unpublished data from Jones and Quenouille at Rothamsted).
- (5) Larvae of a gall midge in grains of wheat (unpublished data from H. F. Barnes).

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## APPENDIX

*Summary of formulae connected with the logarithmic series*

$N$  = total number of units.

$S$  = total number of groups.

$n_1$  = number of groups with one unit.

$\alpha$  = the 'Index of Diversity', a constant for all samples from the same population, if randomized on units.

$x$  = a constant for one sample, always less than unity.

$N/S$  = the average number of units per group.

$n_1/S$  = the proportion of groups with one unit.



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The logarithmic series is

$$n_1, \frac{n_1 x}{2}, \frac{n_1 x^2}{3}, \frac{n_1 x^3}{4}, \text{ etc.,}$$

or

$$\alpha x, \alpha \frac{x^2}{2}, \alpha \frac{x^3}{3}, \alpha \frac{x^4}{4}, \text{ etc.,}$$

I. ( $n_1, \alpha$  and  $x$ ):  $\alpha = \frac{n_1}{x}, \quad n_1 = \alpha x, \quad x = \frac{n_1}{\alpha}.$

II. ( $S, \alpha$  and  $x$ ):  $S = \alpha (-\log_e \overline{1-x}).$

III. ( $S, n_1$  and  $x$ ):  $S = \frac{n_1}{x} (-\log_e \overline{1-x}), \quad \frac{n_1}{S} = \frac{x}{-\log_e \overline{1-x}}.$

IV. ( $S_1, n_1$  and  $\alpha$ ):  $S = \alpha \left( -\log_e \overline{1 - \frac{n_1}{\alpha}} \right).$

V. ( $N, \alpha$  and  $x$ ):  $x = \frac{N}{N+\alpha}, \quad N = \frac{\alpha x}{1-x}, \quad \alpha = \frac{N(1-x)}{x}.$

VI. ( $N, n_1$  and  $x$ ):  $n_1 = N(1-x), \quad N = \frac{n_1}{(1-x)}, \quad x = \frac{N-n_1}{N}, \quad \frac{n_1}{N} = 1-x.$

VII. ( $N, n_1$  and  $\alpha$ ):  $N = \frac{n_1 \alpha}{\alpha - n_1}, \quad \alpha = \frac{N n_1}{N - n_1}, \quad n_1 = \frac{N \alpha}{N + \alpha}.$

VIII. ( $N, S$  and  $x$ ):  $S = \frac{N}{x} (1-x) (-\log_e \overline{1-x}), \quad \frac{N}{S} = \frac{x}{(1-x) (-\log_e \overline{1-x})}.$

IX. ( $N, S$  and  $\alpha$ ):  $S = \alpha \log_e \left( 1 + \frac{N}{\alpha} \right), \quad N = \alpha (e^{S/\alpha} - 1), \quad \frac{N}{S} = \frac{e^{S/\alpha} - 1}{e^{S/\alpha}}.$

X. ( $N, S$  and  $n_1$ ):  $S = \frac{N n_1}{N - n_1} \log_e \frac{N}{n_1}.$

XI. ( $N, S, n_1$  and  $x$ ):  $\frac{n_1}{S} = \frac{N}{S} (1-x).$

XII. The increase in number of groups obtained by multiplying the size of sample by  $p$  when the sample is large (i.e. when  $N$  is large compared with  $\alpha$ ) approximates to  $\alpha \log_e p$ . Doubling the size of the sample therefore adds  $\alpha \log_e 2$  groups. Multiplying the size of the sample by  $e$  ( $=2.718$ ) adds  $\alpha$  groups.

XIII. The variance of  $\alpha$  is  $\alpha^3 \frac{(N-\alpha)^2 \log_e (2N+\alpha/\overline{N+\alpha}) - \alpha N}{(SN+S\alpha-N\alpha)^2}.$

The standard error of  $\alpha$  is the square root of this.

XIV. When  $x=0.633$ , i.e. when the average number of units per group is 1.72,  $S=\alpha$ .

XV. If  $S_1$  and  $S_2$  are the first and second moments of the series:

$$S_1 = N = \frac{n_1}{1-x}, \quad S_2 = \frac{N}{1-x} = \frac{n_1}{(1-x)^2}, \quad \alpha = \frac{S_1^2}{S_2 - S_1}.$$

XVI. The percentage of units in groups containing  $r+1$  or more units is  $100x^r$ . The percentage in groups containing  $r$  or less units is  $100(1-x^r)$ .

# THE INTERTIDAL ECOLOGY OF CARDIGAN BAY

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*(With ten Figures in the Text)*

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## I. INTRODUCTION

Apart from the work of Walton (1915*a, b*), little has been done on rocky shores in Cardigan Bay from an ecological standpoint. Walton's work consisted of some general notes and a list of littoral plants and animals (1915*a*), with a more detailed account (1915*b*) of the distribution of littoral Trochidae and Littorinidae. Some unpublished accounts of local areas by John (1941), David (1941), and Davies (1943) are kept in the University College Library, Aberystwyth, but otherwise Cardigan Bay remains ecologically uninvestigated. Apart from adding to our knowledge of British coasts, a study of the region is likely to provide features of special interest in itself. Walton (1915*a*) records 156 species of littoral animals (including sand-living forms), and this is increased to 201 by Horsman (1922): in comparison with other shores this is poor and apparently consists largely of the more hardy species. Walton attributes the general poverty to three adverse factors, surf action, erosion by loose shifting material and the turbidity of the water. Exactly how such influences act on an intertidal biota is known in a general way only, and a more detailed study should be useful.

The present investigation was made on rock and boulder beaches in the centre of the Bay, and is an attempt to relate the distribution of some of the more common and obvious species to changes in local conditions, mainly those of exposure to wave action and of rock configuration (including the presence or absence of loose material). The vertical zonation of such species is described and compared with results obtained by workers on other parts of the British coasts. Finally, the concept of 'critical levels' and the general features of intertidal zonation are discussed.

## II. CLIMATIC AND TIDAL FACTORS IN THE BAY

The work is confined to the centre of Cardigan Bay (see Fig. 1), from Borth, 5 miles north of Aberystwyth, to a point 5 miles south of the latter town. Consequently, climatic and tidal data for Aberystwyth are taken as applicable.

*Geological.* The region is included in an outcrop of Silurian ('Aberystwyth') Grits, which extends from Borth to Llangrannog. The shoreline consists of an alternation of such rocks with boulder and shingle beaches composed of glacial drift material, with now and then a patch of fine or coarse sand. From Twr Gwyllanod (see map, Fig. 1) which marks the southern limit of the survey the coast runs in a general north-north-eastern direction as a rocky shore, the 'Monk's Cave Rocks', for about a mile, to an area of shingle, boulders, and patches of fine sand, which is referred to as 'Morfa Boulder Beach'. This continues for about 2 miles to the rocky foreshore of 'Alltwn Rocks'. These rocks persist for almost a mile to the storm beach of Tanybwllch. The latter is composed of shingle and is too unstable to harbour a littoral biota, but at its southern extremity occur patches of boulder clay and large boulders, i.e. 'Tanybwllch Boulder Beach'. From Tanybwllch, shingle extends to north of the Harbour mouth as far as the reefs of 'Castle Point', which merge into the lower-lying 'College Rocks'. North of these lies a beach of shingle and coarse sand, interrupted only by the small rocky area known as 'Bath Rocks', until the 'Constitution Hill Rocks' begin, and these extend some  $\frac{3}{4}$  mile to the fine sandy beach of Clarach. Beyond this the 'Clarach-Wallog' rocky foreshore extends a further  $\frac{3}{4}$  mile to 'Wallog Boulder Beach' and 'Sarn Cynfelin', and north of this again the 'Wallog-Borth Rocks', interrupted by small areas of shingle, continues for about 2 miles to the fine sand of Borth beach, which extends without interruption to the Dovey estuary. Thus the survey includes some 10 miles of coastline altogether.

The grits and shales weather differentially into jagged reefs and ledges, strike and dip vary considerably, and the angle of slope ranges from the horizontal to the vertical. Peaks and stacks such as Twr Gwyllanod, Craig y Fulfran (Cormorant Rock), Craig yr Wylfa, and other smaller ones often result from the faulting of previous headlands, the landward portion being washed away to leave mid- or low-tide peaks; also huge loose masses tumble down from the cliff and lie on the foreshore. Chips of shale and slate, shingle, boulders of all sizes, and sand occur throughout. Generally speaking, a shingle beach occupies the upper part of the shore, from about high water of neaps to the base of the cliff, along the entire stretch. The cliff is usually high, up to 300 ft. at Alltwn, and rarely lower than about 50 ft. The slope is precipitous and at most places the cliff base is washed by 12 ft. tides, while both the lower ledges of the cliff and the rocks of the upper shore are frequently smoothed and polished by the moving shingle. The width of the intertidal zone varies from less than 50 yd. (e.g. parts of Constitution Hill Rocks) to over 200 yd. (e.g. College Rocks), and in many places (e.g. near Borth, Castle Point, etc.) high reefs occur at low water, sheltering the lower-lying mid-beach. In places (e.g. parts of Monk's Cave, Clarach-Wallog, and Wallog-Borth regions) rock merges into fine sand at low water, but at other points (e.g. Castle Point, College Rocks) rock extends well into the sublittoral zone. Pools, creeks, gullies, etc., are frequent, and are usually filled with shingle or sand. The irregularity of the rock configuration results in local mitigation of the factors of illumination and surf action, but such variations are only very local, and since the coastline is fairly smooth the region is generally well exposed to breaking waves.

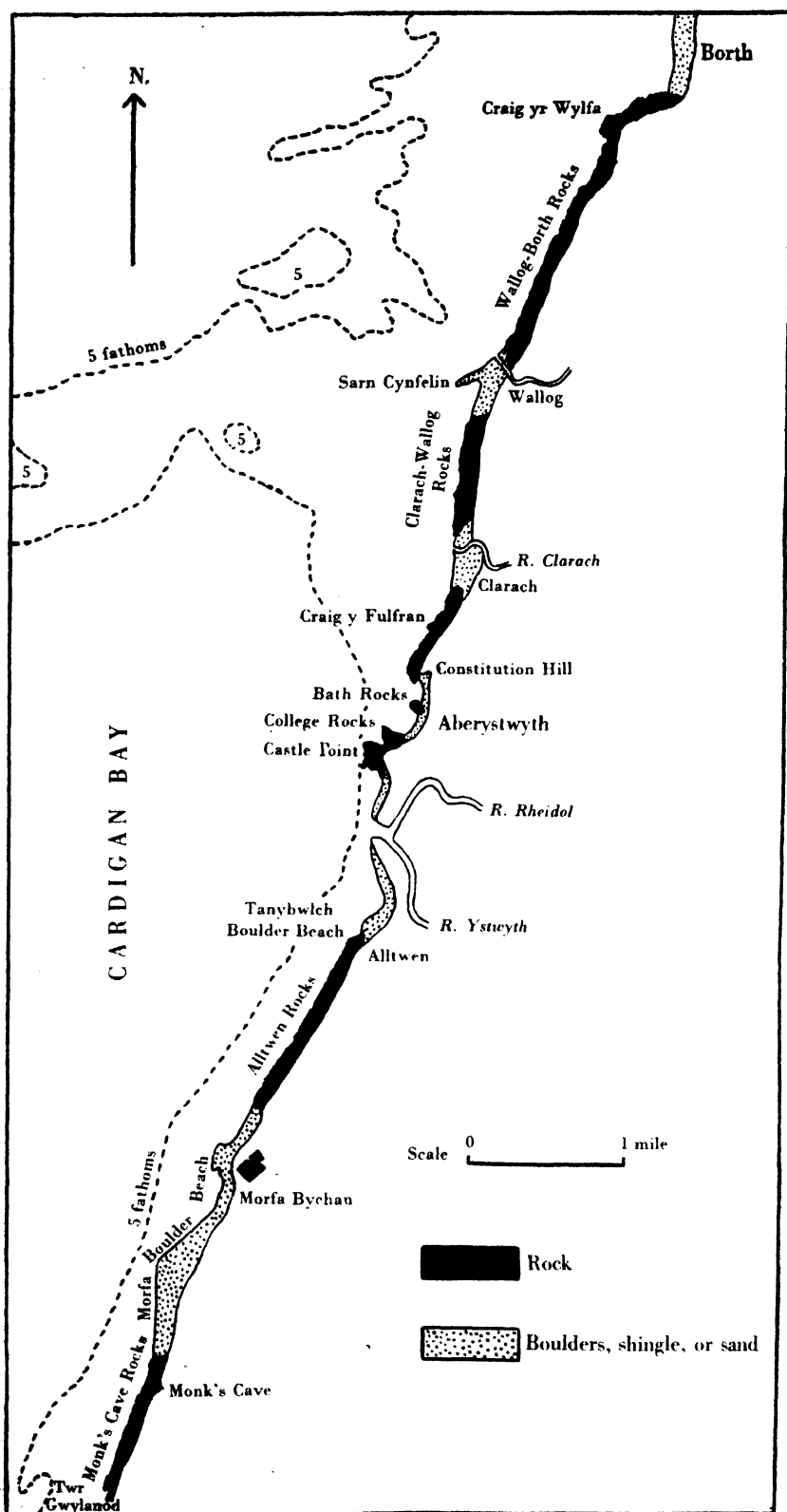


Fig. 1. Map of areas included in the survey.

**Tidal data.** The tides are diurnal, with a range of about 17 ft. at extreme springs and of 5 ft. at extreme neaps; the corresponding times of high or low water are on an average 24 hr. 50 min. later each succeeding solar day, the ebb occupying approximately 7 hr., the flow  $1\frac{1}{2}$  hr. less. Tidal data are calculated from those of the nearest Standard Port which is Holyhead, and according to instructions given in the *Admiralty Tide Tables*, Sect. A, Pts. I and II, and information supplied by the Liverpool Tidal Institute. In reply to a query, the Director of the above Institute writes:

'Your proper procedure would be as follows, taking data from the *A.T.T.*, Sect. A, Pt. II, p. 14. At Aberdovey, M.H.W.N. difference (the average of M.H.W.S. and M.H.W.N.) is  $-1.7$  ft. and at Newquay it is  $-0.2$ . The low water values are  $-0.3$  and  $-0.1$  (?). Thus Aberdovey differences are means of the differences for these two places. Therefore we ought to take:

Holyhead	16.1	12.5	0.2	4.2 ft.
Differences at Aberystwyth	$-2.2$	$-1.7$	$0.0$	$-0.5$ ft.

'If you plot these and draw two straight lines through the values of H.W., and the values of L.W., you can read off the differences to be used for any given height at Holyhead. This procedure can be criticized theoretically for it is known that the differences for tides between springs and neaps differ from those between neaps and springs, and it is somewhat doubtful as to the value of the extrapolation. But in the case of Aberystwyth the principal factor is a change in range only and probably other tidal characteristics can be taken as unchanged throughout Cardigan Bay. You will find that the two straight lines referred to above almost merge, which is an indication (to me) that the proposed method is valid.'

The graph shown in Fig. 2 having been constructed, a tidal scale for Aberystwyth was worked out (Table 1). The heights of extreme springs and neaps are mean values for 1937-46 inclusive, and all heights are referred to Chart Datum in accordance with *A.T.T.*

Cardigan Bay (see Fig. 1) is shallow, and is subject to strong tidal currents. The Admiralty Report states that south-west of Aberystwyth tidal streams run north parallel to the coast as far as the Cynfelin patches (at a rate of 1 knot at springs and 0.5 knot at neaps). Here they meet shallow water about 5 miles offshore, and the tidal stream

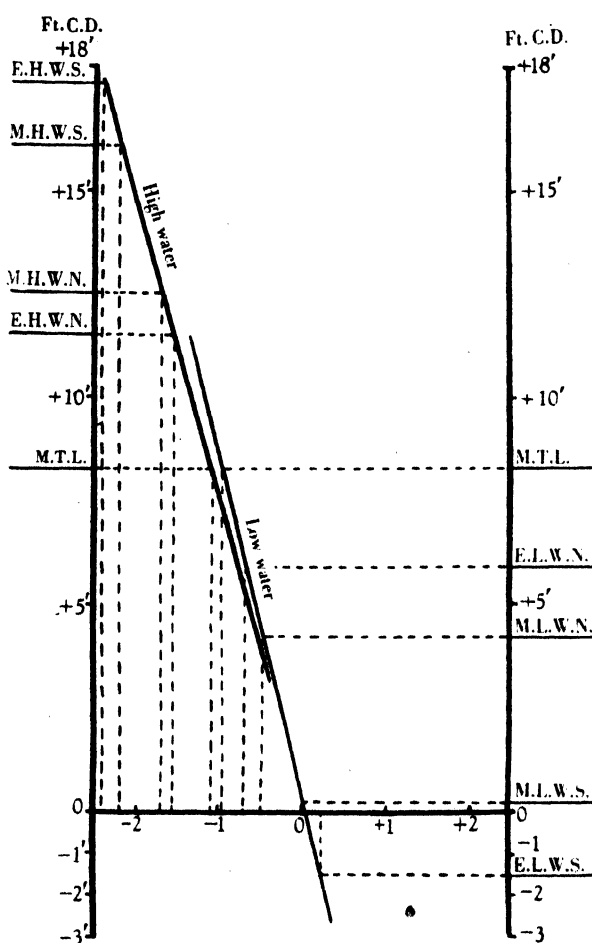


Fig. 2. Method of assessing corrections for Aberystwyth tidal heights from Holyhead data. (For explanation see text.)

is diverted to the east just south of the Patches. This inshore deflexion causes a swifter south-going current to flow past Aberystwyth, independent of and 2 hr. previous to the ebb tide of the offshore waters.

*Wind.* Fig. 3 is a wind rose for the years January 1943 to November 1945. It will be seen that practically 70% of the winds blow from between north-north-east and south-south-west. Winds are generally of strength 1 to 5 (Beaufort scale), and on 20 days per 100 winds of strength 6–12 were experienced. Gales (8–12 strength) are most frequent in autumn and winter, but strong breezes are evenly distributed throughout the year.

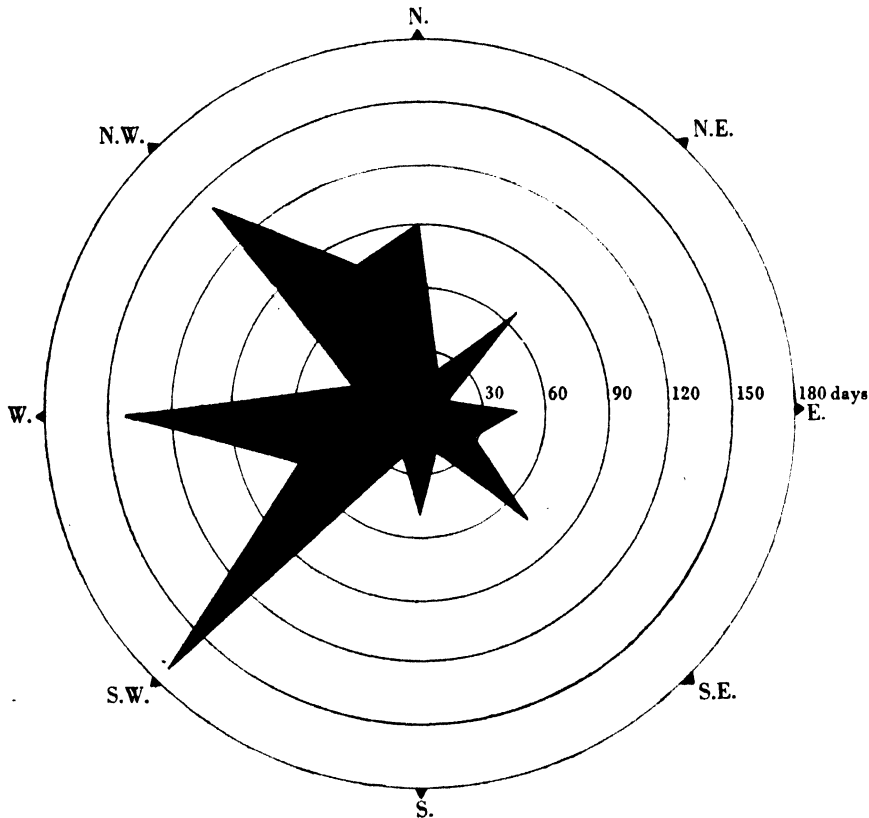


Fig. 3. Wind rose for Aberystwyth, January 1943–November 1945.

*Wave action.* This varies from day to day, and locally in accordance with the sheltering influence of reefs, peaks, headlands, etc. As a result of the set of the tides and the prevailing winds, the western and south-western faces of rocks receive the strongest direct surf, though the whole shore is considerably exposed to it. On the basis of Moore's (1935*a*) calculation for exposure to wave action a factor of 68 is obtained for the centre of Cardigan Bay. Surf action is at its maximum on rocky peaks such as Craig y Fulfran, Twr Gwyllanod, etc., on high seaward reefs, and on the southern faces of headlands. Generally, the northern extremities of rocky stretches (e.g. near Borth, Clarach, Tanybwllch boulder beach) receive shelter from the rocks to the south of them, while College Rocks and, to a lesser extent, Bath Rocks, are sheltered by the high reefs of Castle Point. On a smaller scale, overhangs, depressions and landward faces, in each small area, are sheltered from the full force of the waves. The slope of the shore also has some effect; where this is fairly gentle (e.g. College Rocks) surf action tends to be less violent.

**Rainfall.** Fig. 4 summarizes the distribution of rain for the three years 1943–5 at Aberystwyth. It is fairly evenly distributed throughout the year, the period of minimum rainfall being March–April. The average annual rainfall over the 10 years 1936–45 is approximately 35 in.

**Sunshine.** Monthly totals for 1943–5 are recorded in Fig. 5. April–August is generally the sunniest period, though there is some variation. The lowest spring tides occur in the afternoons, during March–May and September–October, and since the period of minimum rainfall is also March–April then the desiccating effect of sunshine may be important for intertidal organisms at such periods. Rock formation is again important in that it may

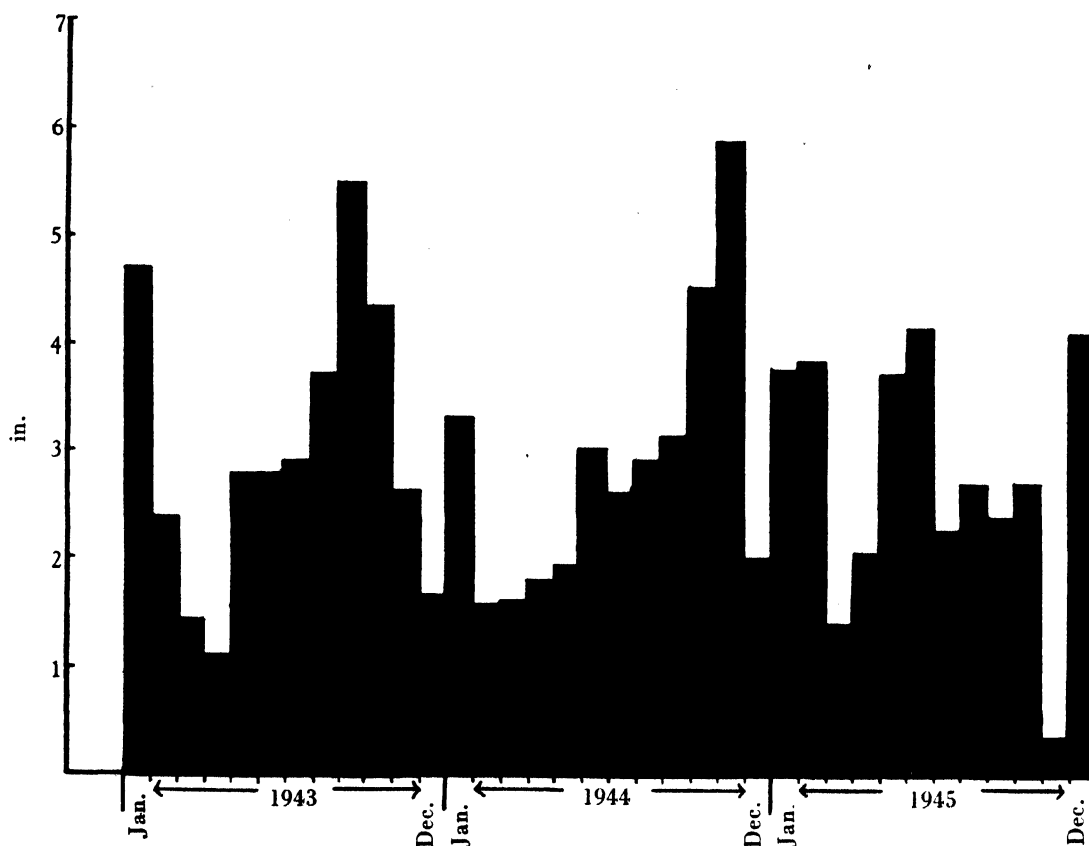


Fig. 4. Monthly totals of rainfall at Aberystwyth, 1943–5.

provide local shade. The high cliff face exerts a considerable shading effect on the upper shore during the early hours of the day, while waves and surf are also important in compensating for evaporation and drying-out.

**Turbidity.** The shallowness of Cardigan Bay, the presence of deposits of sand and mud on the bottom, the swiftly flowing rivers, the strong tidal currents and the heavy wave action all result in the water being generally laden with suspended matter. The effect of this on light penetration and consequently on the metabolism of submerged algae is likely to be important, as Fischer Piette (1936) suggests in the case of *Himanthalia larea*, which has not hitherto been found here, though it occurs further north at Bardsey Island (Pyefinch, 1943).

*Sea temperature.* The temperature of the water will tend to exert a mitigating effect on air temperatures. The mean monthly sea temperatures (1943–5) are shown in Fig. 6, together with the air temperatures, and it is seen that the annual variation is in the neighbourhood of  $20^{\circ}\text{F.}$  ( $11^{\circ}\text{C.}$ ). The water maintains a fairly high temperature well into the winter months.

*Air temperature.* Fig. 6 graphs monthly means, for 1943–5, of maximum and minimum air temperatures. The mean annual range of  $25^{\circ}\text{F.}$  ( $14^{\circ}\text{C.}$ ) is not excessive, and even in the coldest months (December and January) the mean minimum temperature does not

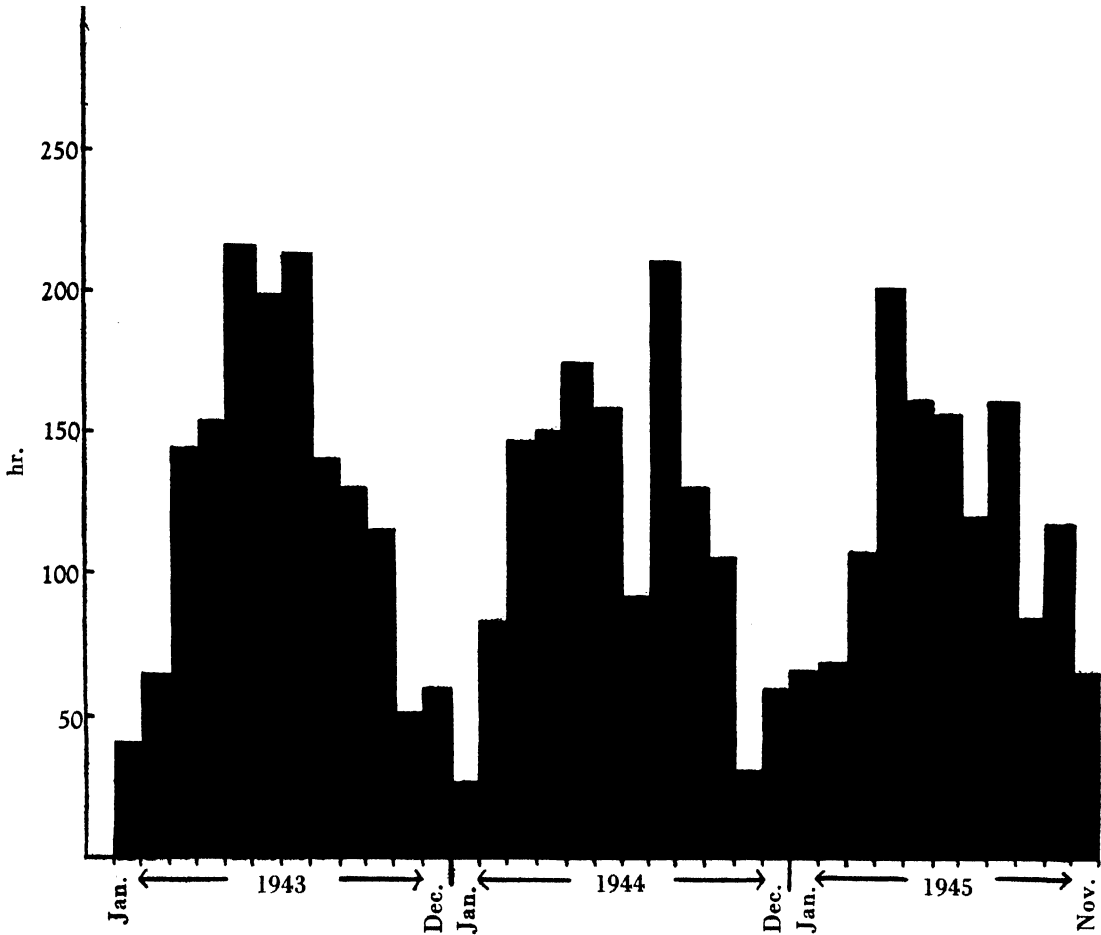


Fig. 5. Monthly totals of sunshine at Aberystwyth, 1943–5.

normally fall below freezing-point. Summer temperatures rarely exceed  $80^{\circ}\text{F.}$  ( $26.5^{\circ}\text{C.}$ ) on any day. Variations in a single day range between  $15^{\circ}\text{F.}$  ( $8^{\circ}\text{C.}$ ) and  $25^{\circ}\text{F.}$  ( $14^{\circ}\text{C.}$ ) on most days, and very rarely do they exceed  $22^{\circ}\text{F.}$  ( $12^{\circ}\text{C.}$ ).

*Salinity.* Salinity determinations of the inshore waters in the Aberystwyth region gave a value of 34.5 parts/1000. Johnston records the 34.5 isohaline for May as extending up into Cardigan Bay. John (1941) describes salinities of 32/1000 on College Rocks, and possibly when the rivers are in flood the effect of the fresh water may be felt along the coast north to College Rocks or even further. Normally, however, the salinity is greater than this, and only slightly lower than full-sea salinities occurring in the open Atlantic.



*Summary.* The climate is typically northern cold-temperature then, and the intertidal region is not subject to great annual variations; generally speaking, conditions may be described as mild.

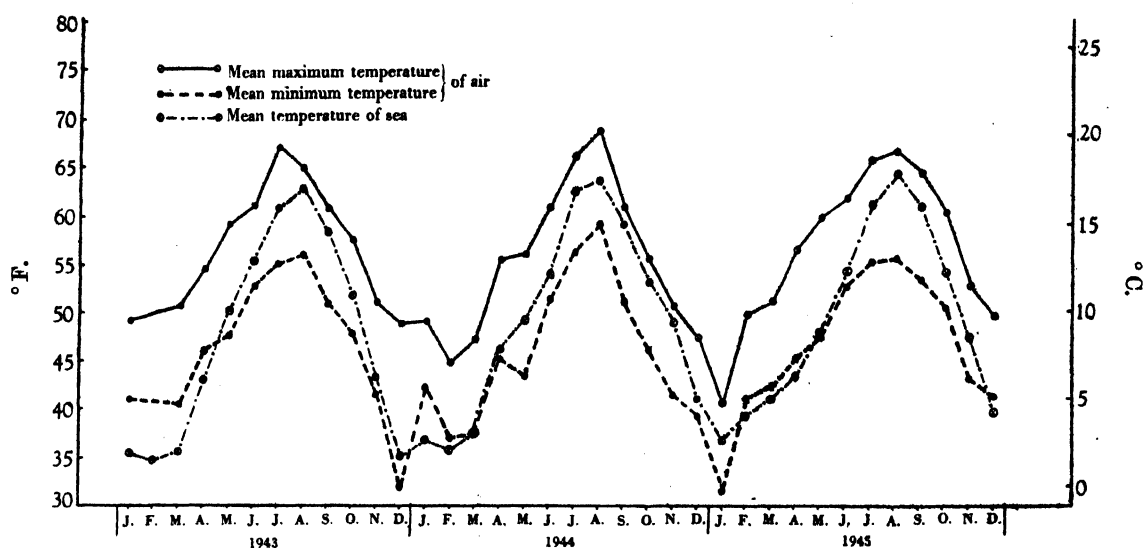


Fig. 6. Mean monthly temperatures of air and sea at Aberystwyth, 1943-5.

### III. TIDAL LEVELS AND EXPOSURE TO AIR

Chapman (1941) and others have described the importance of exposure to the air as a causal factor in vertical zonation, and Colman (1933) has described a method of assessing percentage exposure per year at each level. This method is the one adopted here.

Preliminary graphs illustrating the behaviour of four tides of different range at Aberystwyth were constructed by using Supplementary Table 1, *A.T.T.*, Sect. A, Pt. I, p. 264 and by plotting height against time. All four are typically S-shaped, like those for Wembury (Colman (1933), fig. 7, p. 457).

Next, four fortnights were chosen in 1946, two including high springs and two low neaps, i.e.:

- |                            |                             |
|----------------------------|-----------------------------|
| (a) 21 January-3 February. | (c) 26 April-10 May.        |
| (b) 26 February-13 March.  | (d) 21 November-5 December. |

It will be noticed that I have not chosen the same dates as those used by Colman (1933) since, for 1946 at least, it was thought that the above periods yield the best picture of tidal conditions. For each fortnight the times and heights of high and low water of every tide were graphed, to give figures similar to those of Colman (1933; fig. 12, p. 460). These curves are drawn in freehand as Colman suggests, as it is considered that estimating the hourly height for each tide entails more calculation than is justified by the possibly greater accuracy of the result. From each graph, hours of exposure at each level for the fortnight could be calculated on the squared graph paper on which the curves were drawn. These are given in Table 2, columns *a*, *b*, *c* and *d*. Column *e* gives the total hours of exposure at each level during the four fortnights. By multiplying these figures by the requisite number of days the total hours of exposure at each level for the year can be calculated, and by further dividing by 8760 (=number of hours per year) a percentage figure can be obtained (column *f*). These are represented graphically in Fig. 7. (The tidal levels in this figure for

extreme neaps and springs are 1946 values and not 10-year means, as the graph is based on 1946 tides only.)

Colman (1933; fig. 10, p. 459) has a similar figure to Fig. 7 for Wembury, and Chapman (1941) points out that differences in the rate of change of percentage air exposures from level to level are most marked in the neighbourhood of E.H.W.N. and E.L.W.N. This is also true of the Cardigan Bay graph, and there are also changes between M.L.W.N. and M.L.W.S. (at about 2 ft. above C.D.) and between M.H.W.N. and M.H.W.S. (about 12.5 ft. above C.D.). After describing the horizontal and vertical distribution of the intertidal flora and fauna the possibility that such levels are of critical importance will be discussed.

#### IV. SCHEME AND METHODS

The distribution of the following species has been studied with reference to local variation in environmental conditions, mainly those of exposure to wave action, rock configuration and relationship to other organisms. The nomenclature of the algae follows that of Newton (1931), and the nomenclature for animals that of the *Plymouth Marine Fauna* (2nd ed. 1931).

##### ALGAE

###### Chlorophyceae

- Enteromorpha compressa* Grev.
- E. intestinalis* Link.
- E. prolifera* J. G. Agardh.

###### Phaeophyceae

- Ascophyllum nodosum* Le Jol.
- Fucus serratus* L.
- F. spiralis* L.
- F. vesiculosus* L.
- Halidrys siliquosa* Lyngb.
- Laminaria cloustoni* Edmonst.
- L. digitata* Lamour.
- L. saccharina* Lamour.
- Pelvetia canaliculata* Dene. & Thurs.

##### ANIMALS

###### Crustacea

- Balanus balanoides* (L.)
- Chthamalus stellatus* (Poli)

###### Polychaeta

- Sabellaria alveolata* (L.)

###### Mollusca

- Gibbula cineraria* (L.)
- G. umbilicalis* (da Costa.)
- Littorina littoralis* (L.)

###### Rhodophyceae

- Corallina officinalis* L.
- C. squamata* Ellis.
- Gigartina stellata* Batt.
- Laurencia pinnatifida* Lamour.
- '*Lithothamnium*' (including *Lithophyllum* spp. and *Lithothamnion* spp.)
- Porphyra umbilicalis* J. G. Agardh.
- Rhodomenia palmata* Grev.

##### LICHENS

- Lichina pygmaea* Ag.
- L. confinis* Ag.

- L. littorea* (L.)
- L. neritoides* (L.)
- L. rudis* (Maton.)
- Mytilus edulis* L.
- Nucella lapillus* (L.)
- Osilinus lineatus* (da Costa.)
- Patella athletica* Bean.
- P. depressa* Pennant.
- P. vulgata* L.

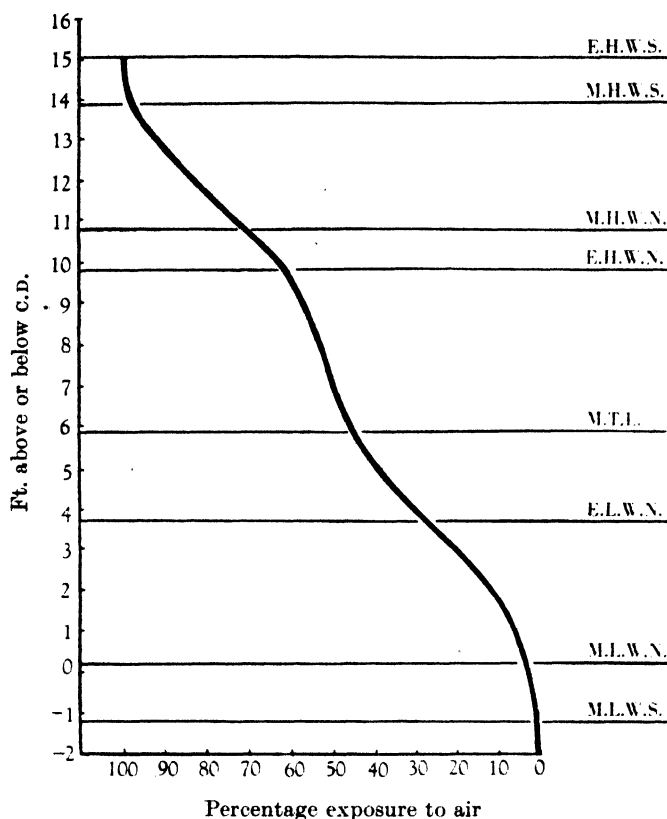


Fig. 7. Percentage exposure to the air at different levels.  
(For explanation see text.)

Some twenty-five areas, covering the range of variation exhibited by local conditions, were chosen for detailed study. These were distributed as follows:

(1)	Rocky mass just south of Twr Gwylanod.	(13)	College Rocks.
(2)	Twr Gwylanod.	(14)	Bath Rocks.
(3), (4), (5)	Monk's Cave Rocks.	(15), (16), (17)	Constitution Hill Rocks.
(6), (7)	Morfa Boulder Beach.	(18)	Craig y Fulfran.
(8), (9), (10)	Alltwen Rocks.	(19), (20)	Clarach-Wallog Rocks.
(11)	Tanybwllch Boulder Beach.	(21)	Wallog Boulder Beach.
(12)	Castle Rocks.	(22), (23), (24)	Borth-Wallog Rocks.
		(25)	Craig yr Wylfa.

These areas varied in size, being never less than 50 yd. wide, and all extending down to low water. Observation was not entirely confined to the areas listed, but supplemented by more general observation along the entire coast. Such a wide survey, while sacrificing some of the accuracy possible in detailed studies of small areas or traverses (e.g. Colman (1933), Hewatt (1937)), nevertheless yields a more useful general picture of distribution, as Stephenson (1941) has remarked. It will be noticed too that reference is made to the distribution of the various organisms in South Devon. Localities in this area, including Church Reef, Wembury, on which Colman (1933) worked, have been studied on the same lines as Cardigan Bay. The results of this study form the material for a subsequent paper.

Tidal levels on each area were marked by observation, and the method of marking demands some description and comment. While accurately surveyed and labelled traverses are indeed useful, they fail to take into account the effective level of tides as determined by the 'wash, splash and spray zones' (Stephenson, Bokenham & Neugebauer, 1938). These vary so much locally that the addition, to predicted tidal levels, of an average height for splash, as suggested by Colman (1933), is probably only justifiable on a small scale survey such as his. The lack of surveyed traverses need not hamper work between tide marks, and it is believed that the method used in the present work allows of a more extended survey and results in a better picture of intertidal conditions. Direct observation of tidal heights involves the use of Supplementary Table 1, *A.T.T.*, Sect. A, Pt. I, in order to calculate the hourly rise and fall of the tide, and demands certain precautions:

(a) A calm day is necessary.

(b) The actual time of the preceding high and succeeding low tide must be checked against the predicted times. The absence of a tide gauge at Aberystwyth, or of any suitable structure on which a rough gauge or tide-pole could be attached, makes it impossible to check predicted heights. The choice of a calm day, however, tends to offset any great variation from the prediction, and in *A.T.T.*, Sect. A, Pt. II, p. viii, it is stated, 'In open waters changes in sea level due to wind seldom exceed 1 ft.'

(c) Levels must be checked by observation on different days and at different states of the tide (springs and neaps).

In practice, the method works as follows. Starting from the time of high water the area is horizontally traversed, along the water line, every half hour during the first and last 90 min., and every quarter hour during the middle hours, of the ebb tide. Notes on the presence or absence, on the relative abundance, and on the features of distribution of the chosen species are taken during each traverse. The height at which each traverse was taken can later be calculated by using, once again, Supplementary Table 1, and the vertical

zonation of each species worked out. Each area is later checked. It was also found useful to employ a graduated staff and plumbline for measuring heights on vertical peaks and on the cliff face, while the heights of the 'barnacle-line' and of easily recognizable peaks and artificial structures (e.g. breakwaters) were found useful as reference points.

The general close agreement between the results indicates that the method has a good degree of accuracy. On the cliff face of Constitution Hill, the height of the barnacle-line was assessed as 13.5 ft. above C.D., while some years ago (Rees, 1941) it was levelled by accurate survey at 13.6 ft. Moreover, during the survey of localities in South Devon similar methods were employed, and a very close agreement was found between results obtained for the position of algal zones on Church Reef and the results of Colman (1933) on the same area. Thus the method would appear to sacrifice little by dispensing with surveyed levels.

## V. RESULTS

The following descriptions and notes summarize the distribution of the species studied in the twenty-five different areas.

### A. *Flora*

*General distribution of algae.* Generally speaking, fucoids are poorly developed along the whole coast, but considerable variation is encountered, related to (a) the intensity of exposure to wave action, and (b) rock formation. In a few places only (e.g. College Rocks) the weed associations are very well developed, the rocks being carpeted with algae; at the other extreme (e.g. Twr Gwyllanod) such cover is totally absent. Between these extremes exist numerous intermediate states, with fucoid communities in various stages of development. Exposure to surf is very obviously a prime determinant of the amount of fucoid growth. College Rocks are not only sheltered from the south and south-west by the high rocks of Castle Point, but also the mid-beach is sheltered to some extent by the presence of reefs at low water. The long gentle slope of the shore at this point also results in surf being less violent. Algae are affected by wave action in three principal ways: (a) they are torn off the rock unless they have a strong and efficient holdfast; (b) the mechanical effect of excessive surf pounding on the thallus is destructive to it; (c) algal spores settle less readily in rough conditions. The slope and texture of the rock surface will be important not only directly to the settling spores, but the angle of the slope will itself affect the wave shock, sometimes reducing or modifying it and sometimes not. Thus rock configuration is important, and its effect in providing local shelter results in variation along the coast in the amount of fucoid growth. The protective effect of outer reefs, for instance, often allows fucoids to grow well to landward of them in an otherwise surf-beaten locality. On the other hand, even in a fairly sheltered area such as College Rocks, rocky peaks and protruding ledges tend to be bare of weed though surrounded by a thick carpet. Similar effects of surf and rock slope have been recognized by other authors, e.g. Rees (1935), Cotton (1912), Gislén (1929), etc.

The presence of loose material (sand, pebbles, etc.) which can be moved by the sea is usually an adverse factor, and was noted at Aberystwyth by Cotton (1914, p. 36). Its presence accounts for the absence of fucoids in many fairly sheltered areas which would otherwise be suitable for them, especially at the top of the shore and on the lower cliff face. On the other hand, fucoids sometimes grow well on immovable boulders in fairly sheltered places (e.g. northern end of Constitution Hill Rocks, Tanybwllch Boulder Beach). The effect of moving material is partially direct, in its mechanical effect on adult thalli and in

scraping spores and sporelings off the substratum, and partially indirect, in polishing the rock and increasing the difficulty experienced by settling spores in obtaining a foothold. The size of the loose stuff naturally decides the ease and frequency with which it is moved, the quality of the material (shingle, gravel or fine sand) affects its efficiency as a polishing and scouring agent, and fine sand and silt are not particularly harmful to fucoids. Indeed, the deposition of these materials on the rock may even favour algal growth; in many places (e.g. rocks abutting on Clarach sandy beach) silt encourages such weeds as *Enteromorpha*, which pave the way for subsequent colonization by fucoid algae.

The patches of sand tubes made by *Sabellaria alveolata*, which is common in the region, provide an excellent substratum, and in addition to sporelings of *Fucus* these cushions are often covered with a thin algal 'turf', including such species as *Corallina officinalis*, *Laurencia pinnatifida*, *Enteromorpha prolifera* (and other *Enteromorpha* species), *Chaetomorpha crassa*, *Ceramium rubrum*, *Lomentaria articulata*, *Dictyota dichotoma*, *Ulva* sp., etc., while at low tide levels *Rhodymenia palmata*, *Corallina squamata*, *Laminaria* sporelings, *Gigartina stellata*, and lithothamnia are common in this habitat.

Different algal species clearly have different ranges of tolerance toward the adverse factors of surf action, unfavourable slope of the rock, and smoothness of substratum. Thus small algae such as *Corallina*, *Laurencia*, *Gigartina* and the calcareous encrusting forms are far more tolerant of surf than are the larger fucoids, while *Enteromorpha* and *Porphyra umbilicalis* may occupy smooth rock and boulders which are not colonized by any other algae.

The considerable variation and irregularity of the foreshore result in a very discontinuous horizontal distribution of algae. It is difficult to cite specific examples, but the general impression one gains is that, between an extremely wave-beaten and weed-free locality such as Twr Gwyllanod and a fairly sheltered fucoid-covered area such as College Rocks, there exists a continuous series of intermediates. It is the lower and upper shore which first tend to become colonized by fucoids as shelter increases (unless local effects such as an outer reef sheltering the mid-beach complicate matters), and the mid-tide region is the last to be well covered. This process is observed with far more clarity on an irregular coastline such as that of South Devon, where a series of localities exhibiting regular improvement of shelter can be chosen. The phenomenon will be discussed in detail in a subsequent work dealing with these localities.

The negative correlation between fucoid and barnacle distribution noted by several workers is well shown in Cardigan Bay, and predominantly 'barnacle areas', predominantly 'fucoid areas' and 'mixed areas' can be distinguished. The effect of barnacle-encrusted surfaces on isolated algae which do manage to survive on such wave-beaten rock is commonly very marked; the algal fronds, rubbing over the surface, are tattered and often worn down to very short stumps. Such an effect is also noted by Hatton (1938). The reverse effect of *Fucaceae* on barnacles will be discussed later.

*Pelvetia canaliculata*. The presence of shingle on the upper beach and the general instability of the cliff face do not encourage any extensive development of a *Pelvetia* zone in the region, while on most of the midtidal peaks the adverse action of surf is frequently too marked to allow the alga to develop. Authorities such as Kitching (1935), Rees (1935), Hatton (1938), Gibb (1938, 1939), and others, agree that while *Pelvetia* occurs from positions of extreme shelter to those of moderate exposure, under the latter conditions it requires rough or much-fissured rock. The species is at its best here on large table-like

masses at the cliff foot in the Monk's Cave region, and at heights above the limits of the abrasive action of shingle. Even here, the alga favours the shelter of ledges and the north aspects of such rocks, unless they are sheltered by peaks in front, and it is always thickest where the surface is roughest. North of Monk's Cave to Borth *Pelvetia* is very discontinuous in its distribution; occasional patches only occur (e.g. on a reef on the landward side of Craig y Fulfran, and on the cliff face at the north end of Constitution Hill Rocks).

The '*Pelvetia* zone' can be described as extending from just below M.H.W.S. to just below E.H.W.S., but the alga occurs thinly from E.H.W.S. down to M.H.W.N. + 1 ft. in places. A small patch occurs behind ledges on the west face of Craig y Fulfran, and here *Pelvetia* is found between E.H.W.S. + 1.5 ft. and E.H.W.S. + 4 ft., which is presumably due to the great height of the splash zone.

Colman (1941) comments on the non-mixing of *Pelvetia* and *Fucus spiralis*; in Cardigan Bay both may be found mixing freely in many places where neither alga is particularly thick. On rock masses near Monk's Cave a definite mixed community of both algae is quite common.

*Fucus spiralis*. Although the zone normally occupied by this alga lies within the range of the shingle beach, it is rather lower in distribution than *Pelvetia*, and in places (e.g. College Rocks) the lower part of the *Fucus spiralis* zone at least is represented on the upper shore. Where it is able to withstand surf conditions, *F. spiralis* appears to be more tolerant of loose material than *Pelvetia*, and on Tanybwllch Boulder Beach plants thrive where the underlying rock is completely covered by shingle. *Fucus spiralis*, too, occurs on peaks and masses at the top of the shore, generally best on gentle slopes, on rough rock, and on north-eastern aspects. Its absence from some localities (e.g. Craig y Fulfran) where *Pelvetia* is present, seems to indicate that it is less tolerant of surf than the latter, which agrees with Kitching's (1935) observation on the Argyllshire coast. Cotton (1912), however, considers it to be more tolerant than *Pelvetia*.

On the topshore masses near Monk's Cave, on the landward side of College Rocks, on flat beaches near Borth and in a few other places, a '*Fucus spiralis* zone' may be recognized, and usually extends from E.H.W.N. up to M.H.W.S. - 1 ft. The species may straggle outside this from E.H.W.N. - 1.5 ft. to M.H.W.S., while in one area near Borth *F. spiralis* sporelings up to 4 in. in length were found on a patch of *Sabellaria* as low as M.T.L. This last record is surprising, but it is interesting to note that Zaneveld (1937) records the alga to M.T.L., and so does Grubb (1936) at Peveril Point, Dorset.

Several authorities have commented on the non-mixing of *Fucus spiralis* and *Ascophyllum nodosum* zones. Very little mixing does occur, especially where both algae are thick, but *Ascophyllum* is occasional to M.H.W.N. in the *Fucus spiralis* zone and the latter to 1.5 ft. below the upper limit of *Ascophyllum* (e.g. on College Rocks).

The underflora of the *Fucus spiralis* community is generally poor and the rock is bare, but where mud or silt are deposited (e.g. College Rocks, Tanybwllch Boulder Beach) it is common to find small sand communities, including *Enteromorpha compressa* and species of *Cladophora* and *Gelidium*.

*Ascophyllum nodosum*. This is very unevenly distributed throughout the region. On the Monk's Cave Rocks there is but one locality, of lower rock sheltered by high reefs, where *Ascophyllum* is developed at all; on the Alltwen stretch it occurs only on the north end, near Tanybwllch; from Constitution Hill to Borth occasional patches are found, though sometimes (e.g. near Clarach and just south of Craig yr Wylfa) these may be fairly thick.

On Castle Point *Ascophyllum* is frequent, and the individual plants are robust and long-fronded behind the outer reefs, but a thick carpet is not achieved. On Bath Rocks the alga is again local behind reefs and ledges. On College Rocks a thick carpet, over 100 yd. wide from top to bottom, of long-fronded and robust plants is developed. From the survey it appears that the *Ascophyllum* community requires a long, fairly level beach, with shelter from surf; such conditions are best fulfilled, in this region, on College Rocks. Hatton (1938) says that on very rugged rocks the alga requires a thin film of mud; this too is plentiful on College Rocks. Borgesen (1908) in the Faeroes, and Zaneveld (1937) at Den Helden, conclude that *Ascophyllum* is more tolerant than *Fucus vesiculosus* of the adverse effects of surf, but most authorities take the opposite view, and Kitching (1935); Cotton (1912), Rees (1935), Gibb (1938), and others all cite *Ascophyllum* as demanding more sheltered conditions. This appears to be the case at Aberystwyth, an observation also made by David (1941). Curiously enough, it is common to find adjacent, flat, exposed reefs just above M.L.W.N., both with a thick barnacle cover and few fucoids, and with no obvious differences in rock slope, texture, or exposure to wave action, yet on one *Fucus vesiculosus* is the only alga, on the other the occasional and battered plants are those of *Ascophyllum*. Though intolerant of direct wave shock, *Ascophyllum* is often well represented along channel banks where the current is strong; Elmhirst (1933) comments on the suitability of the long, elastic, and stream-lined fronds of the species to withstand the prolonged drag of currents.

Though it may occur on steep slopes and overhangs where these are protected, *Ascophyllum* prefers a gentle or horizontal slope, as Zaneveld (1937) and Gislén (1929) both note. Furthermore, it is rare on stones or boulders, being much less tolerant of such a habitat than is *Fucus vesiculosus*. *Ascophyllum* is also very susceptible to the scouring effect of loose material, and it is common to find plants inhabiting cracks in polished rock with their fronds worn down level with the rock surface and frequently no more than a centimetre or so long.

Where the alga is thick the upper limit of the *Ascophyllum* zone is well marked at about E.H.W.N., with occasional plants to M.H.W.N. The absolute lower limit anywhere is no lower than M.L.W.S. + 2 ft., but on the south edge of College Rocks the alga is thick to this level, mixing with *Fucus serratus*. At most localities the *Ascophyllum* community merges into one of *Fucus vesiculosus* and barnacles well above this level, due to the adverse effects of surf in mid- and low-tide regions.

A well-developed *Ascophyllum* community has, normally, a thick undergrowth including *Sabellaria*, lithothamnia, *Ulothrix flacca*, *Cladophora rupestris*, *Chaetomorpha crassa*, *Enteromorpha* species, *Corallina officinalis*, etc. Lower down, such species as *Rhodymenia palmata*, *Ceramium rubrum*, *Lomentaria articulata* and *Laurencia pinnatifida* are common.

*Fucus vesiculosus*. Though far more frequent in the region than *Ascophyllum*, *Fucus vesiculosus* never exists anywhere in as dense a cover as *Ascophyllum* does on College Rocks. It is most profuse in small areas of lower rock on the Monk's Cave stretch, but even here it is never very thick. Usually, it is common where *Ascophyllum* is good, and is sparse (but generally better than the latter species) on exposed areas. David (1941) suggests that, in Cardigan Bay at least, there exists a delicate balance between these two fucoids, controlled by factors of rock slope and exposure to wave action. The present worker is inclined to the same view, and would add that *Fucus vesiculosus* appears to have

certain optimum requirements of surf for thick growth; at intensities of wave action above this optimum barnacles are dominant and *F. vesiculosus* is sparse, and when the intensity of surf falls below this optimum *Ascophyllum* is allowed to be present and tends to dominate the other. This would explain the infrequent occurrence of a rich, pure carpet of *Fucus vesiculosus*. When present on exposed rock *F. vesiculosus* plants are invariably scrubby and tattered, frequently worn down to the mid-rib, and in such a condition they appear to be very susceptible to epiphytic growth. The species seems to be rather more tolerant of sand, etc., than *Ascophyllum*, and plants are often found on sandy beaches attached to the underlying rock which may lie a foot or more below the surface. While it is able to colonize smaller stones and boulders to a greater degree than *Ascophyllum*, *Fucus vesiculosus* too is finally limited by the size of such stones.

The upper limit of distribution is slightly lower than that of *Ascophyllum*, and *Fucus vesiculosus* is rarely found above E.H.W.N. except when this limit is raised by splash. On Morfa Boulder Beach it is occasional as low as M.L.W.S. + 1 ft., i.e. to a slightly lower level than *Ascophyllum*. The zone of abundance of *Fucus vesiculosus* is variable; its upper limit of abundance may be determined by competition with *Ascophyllum*. Thus at Castle Point both algae are common from E.H.W.N. down; where *Ascophyllum* is absent *Fucus vesiculosus* is dominant from E.H.W.N.; on the north edge of College Rocks it is dominant from about M.T.L. down only, as *Ascophyllum* disappears with decreasing shelter; on the south side of College Rocks it is never dominant, as *Ascophyllum* is the dominant alga of the mixed community right down to the beginning of the *Fucus serratus* zone. Similarly (see later), the height of the *F. serratus* zone influences the lower limit of dominance of *F. vesiculosus*.

*Fucus serratus*. In many localities this is the best developed fucoid, for whereas the mid- and upper-beach may be poor in algal cover, there is usually a fringe of *F. serratus* near low water unless the shore ends in steep rocky reefs (e.g. Castle Point). It definitely shuns steep slopes unless these are very protected, and prefers level rock, as described by Cotton (1912) and others. Even on horizontal rocks, *F. serratus* is poor if surf is very strong (e.g. many places in the Constitution Hill area). The species grows fairly well on boulders (e.g. at Wallog), and like *F. vesiculosus* it is tolerant of fine sand.

Where conditions of rock slope and exposure to wave action are both suitable there is usually an excellent zone of *F. serratus* on the lower beach, but the height to which this zone extends is variable. On very steep exposed faces (e.g. Twr Gwyllanod) there is no zone; on fairly exposed flat rocks it may extend to 1 or 2 ft. above M.L.W.S. (e.g. south end of Constitution Hill Rocks); on the north of College Rocks it is common from M.L.W.N. down; in places near Borth *F. serratus* is the dominant alga from M.T.L. - 1 ft. down. Increasing shelter, then, raises the upper limit of dominance of *F. serratus*, but only up to a point. Once surf action is sufficiently reduced to allow *Ascophyllum* to develop this may be co-dominant with *Fucus serratus* as low as M.L.W.S. + 2 ft. (e.g. south side of College Rocks). Correlated with the upper limit of *F. serratus* dominance is the lower limit of abundance of *F. vesiculosus*, and between M.T.L. and M.L.W.S. + 2 ft. one can visualize a competition between these three species, *F. vesiculosus*, *F. serratus* and *Ascophyllum*, a competition influenced by factors of rock slope and exposure to wave action. In all cases the lower limit of *Fucus serratus* lies below M.L.W.S. and the alga mixes with the laminarians, but it shows a definite tendency to die out towards E.L.W.S.

The undergrowth of the *F. serratus* zone commonly includes *Sabellaria*, *Corallina* sp.,



lithothamnia, *Laminaria* sporelings, *Rhodymenia palmata*, *Lomentaria articulata*, *Ceramium rubrum*, *Gigartina stellata*, *Plocamium coccineum*, etc.

*Laminarian zone.* Three species of *Laminaria* are common in the region, *L. digitata*, *L. cloustoni* and *L. saccharina*, and these are characteristic of levels below M.L.W.S. The 'Laminarian zone' is generally well developed, except (a) where rock is replaced by sand at low water, or (b) on vertical, very wave-beaten surfaces (e.g. Twr Gwyllanod, Craig yr Wylfa, etc.). Rees (1935) states that *L. digitata* never occurs on precipices, but at Aberystwyth it is common on vertical faces when these are protected (e.g. in rocky clefts, on gully banks or on landward faces). The upper limit of this zone dominated by *Laminaria* generally lies in the region of M.L.W.S. (e.g. Tanybwllch Boulder Beach, parts of the Constitution Hill Rocks, in the centre of the Wallog-Borth area), but where splash is great the zone may begin as high as M.L.W.S. + 1 ft. (e.g. Bath Rocks, seaward extremity of College Rocks, south flank of Constitution Hill Rocks).

*L. digitata* has the highest upper limit, and is sometimes taken to 3 ft. above C.D. (i.e. M.L.W.N. - 0.7 ft.). *L. Cloustoni* rarely occurs above M.L.W.S. but improves towards E.L.W.S., and is especially good on exposed points. *L. saccharina* prefers more sheltered conditions than the other two (e.g. north-eastern side of College Rocks), and occurs from M.L.W.S. down; on exposed reefs it is generally confined to pools. All three species extend below E.L.W.S. into the sublittoral.

The undergrowth of the Laminarian zone is largely composed of sheets of lithothamnia, *Rhodymenia palmata*, *Corallina squamata*, *Cladophora* sp., *Fucus serratus*, *Gigartina stellata*, *Plocamium coccineum*, etc.

*Rhodymenia palmata.* This is one of the commonest red algae at low-tide levels, and occurs on rock, on *Sabellaria*, and as an epiphyte on *Fucus* and *Laminaria cloustoni*. In some places it is the dominant large alga from about M.L.W.S. + 2 ft. down to the *Laminaria* zone, in more protected areas it is characteristic of the undergrowth of *Fucus serratus*. The upper limit of *Rhodymenia palmata* is generally just above M.L.W.N., but under a thick fucoid carpet it may persist almost to M.T.L., while the lower limit lies beyond tide marks. *Rhodymenia* may be locally poor or absent (e.g. Wallog Boulder Beach and a few areas north of this) for no apparent reason.

*Laurencia pinnatifida.* Like *Rhodymenia*, this species is again commonly associated with cushions of *Sabellaria*, and its short, scrubby fronds are one of the main constituents of the 'algal turf' previously mentioned. Cotton (1912), Rees (1935), Kitching (1935), Gibb (1938, 1939) and others all recognize a '*Laurencia* association' on exposed and moderately exposed coasts, and Cotton (1912) states that it is best on flat or gentle slopes. In Cardigan Bay, *Laurencia* appears to be more tolerant than the fucoids of surf action, but it is normally short in growth and best on flatter rocks and landward slopes. It is never found forming an extensive carpet as it is reported to do on other shores (e.g. Rees, 1935, at Lough Ine). From Clarach to Borth, *Laurencia* is less frequent than it is from Clarach to the south; possibly this is due to the effect of loose sand, which Cotton (1912) describes as harmful to this species.

The alga is found occasionally to just below E.H.W.N., and on one rocky peak near Twr Gwyllanod, and exposed to heavy wave action; mixed patches of *Laurencia* and *Lichina pygmaea* were observed in crevices as high as E.H.W.N. Generally speaking, however, *Laurencia* is best from M.T.L. to M.L.W.S., and below this level it dies off to E.L.W.S.

*Corallina*. While both *C. squamata* and *C. officinalis* occur in the region, the latter is the more frequent, and the former species is confined to low-tide levels. *C. officinalis* occurs in clean, fucoid-free pools on peaks and headlands to above M.H.W.S., and on patches of *Sabellaria* under a thick fucoid carpet to E.H.W.N., but on the open shore it is more characteristic of levels below M.T.L. Here it is common in pools and outflows, on *Sabellaria*, on barnacle encrusted rock, or on sheets of lithothamnia. Cotton (1912) describes the 'Corallina association' as typical of exposed coasts, replacing the 'Laurencia association' when surf is too intense for the latter, and in Cardigan Bay *Corallina* is obviously one of the most tolerant of the littoral algae with regard to wave action. Where steep reefs occur at low tide, it is frequently the only alga present in quantity, and on such reefs (e.g. College Rocks, Castle Point, south flank of Constitution Hill, etc.) a definite 'Corallina-Balanus community' can be recognized, with few, if any, tattered fucoids. Such a community is general from M.L.W.N. to M.L.W.S. in places; beyond M.L.W.S. *Balanus* dies out, but *Corallina* continues to E.L.W.S. either with *Sabellaria* or as a 'Corallina-lithothamnia association' on very exposed rocks.

In pool outflows both *Corallina* and lithothamnia are frequent, and the former often traps suspended matter in the outflowing water. The resulting deposit of sand and silt may be colonized and added to by *Sabellaria*.

'Lithothamnia.' The writer has not attempted any specific identification of the encrusting calcareous algae, but according to David (1941) the species occurring on College Rocks are: *Lithothamnion lenormandi* (M.S.L. to E.L.W.N.), *L. polymorphum* (E.L.W.N. to M.L.W.S.), and *Lithophyllum incrustans* (at low tide and in pools).

Such algae are typical of clean fucoid-free pools and are commonly associated with *Corallina*. On rock and on *Sabellaria* under fucoids, in damp depressions, pools and pool outflows, lithothamnia extend well up the shore, but it is in the *Laminaria* zone that they are best developed, spreading over exposed rocks in extensive pink sheets. The encrusting habit and life form of such species ensure a wide range of tolerance of surf, and it is common to find ledges and precipices at low tide on which lithothamnia are the only surviving algae.

*Gigartina stellata*. Most workers describe a 'Gigartina association' on moderately wave-beaten coasts, but in the centre of Cardigan Bay it is uncommon to find *Gigartina* actually dominating a community. It is typical of the lower shore, and is frequent from M.L.W.S. +1 ft. down in the *Fucus serratus* and *Laminaria* zones, while occasionally it may be taken as high as M.L.W.N. (e.g. College Rocks). From Wallog to Borth, *Gigartina* is, for some reason, very occasional and was only taken in quantity in one small area. The lower limit lies below E.L.W.S. On the boulder beach at Aberayron, south of Aberystwyth, *Gigartina* thrives, and is one of the most common algae on such a beach.

*Porphyra umbilicalis*. With regard to the intensity of surf action and the texture of the substratum, this alga is extremely tolerant, occurring on both sheltered and barnacle-encrusted rock faces, on sand, on smooth boulders and ledges (frequently together with *Enteromorpha*) and as an epiphyte on *Fucus*. *Porphyra* is, however, very local in its distribution and is best seen in winter and early spring.

In its vertical distribution, too, *Porphyra* displays considerable tolerance to factors of submergence and emergence. Borgesen (1908) records it to 50 ft. above H.W.M., and on Twr Gwylaned it was found up to 4 ft. above E.H.W.S. From here down it is sporadic in occurrence to the Laminarian zone. Grubb (1924), Rees (1935), and others describe *Porphyra* as extending to low water.

*Enteromorpha*. Species of this alga are widely distributed on the shore. Patches of *E. compressa* are common above tide marks on the cliff face where free water oozes through cracks in the rock, and the same species often forms an association (frequently with *Porphyra*) on the smooth boulders and polished ledges of the upper beach, and in similar habitats lower down. *Enteromorpha prolifera* is common on *Sabellaria* cushions and as an undergrowth in fucoid zones, and the same species may be epiphytic on *Fucus*. *Enteromorpha intestinalis* is characteristic of pools and damp situations generally. *Enteromorpha* is one of the primary colonizers of silt and mud deposits, and, as Hatton (1938) describes, aids in the subsequent colonization of such surfaces by fucoid algae.

*Halidrys siliquosa*. This is by no means common in the region, and from its restriction to quiet pools (e.g. Pwll Padarn, on College Rocks) it would appear that surf conditions on the open coast are too pronounced for the species.

*Lichina pygmaea*. The lichen is discontinuous in its distribution, and this is influenced by the same factors in Cardigan Bay, as workers such as Rees (1935), Cotton (1912) and Naylor (1930) have described as important elsewhere. It favours wave-beaten situations, and is best developed on vertical or steep southern or south-western slopes (e.g. the southern faces of Craig y Fulfran, Twr Gwylanod, etc.), but its presence (often as thick patches) on overhangs, on northern and north-eastern faces, and on horizontal rock suggests that the growth of the species is favoured by water movement in general, and not only by direct wave shock. A rough substratum is preferred, and *L. pygmaea* is most extensive on rock thickly covered with barnacles, or in cracks, or often around the bases of solitary fucoids on exposed reefs. In many places (e.g. Castle Point), where conditions of exposure and substratum seem to be fulfilled, *L. pygmaea* is unaccountably absent. Naylor attributes a two-fold effect to surf action: (a) active mechanical stimulus, and (b) aeration. In addition, the writer would suggest that surf has also two indirect effects: (a) in encouraging barnacles, and so providing a rough substratum, and (b) in removing the possibility of algal competition.

The effect of illumination is doubtful; Naylor (1930) discusses the possible need of the thallus for drying-out during periods of exposure to the air, and remarks that the lichen is best developed on southern and illuminated faces at Plymouth. However, both in Cardigan Bay and at Plymouth, the present worker has observed rich growths of *L. pygmaea* on permanently shaded surfaces, under overhangs, and in damp cracks and holes, while Rees (1935) describes it as growing most luxuriantly in damp depressions. Provided that water movement is sufficiently strong the species can remain permanently shaded, and illumination seems to be of secondary importance, if any. The fact that it is often most extensive on southern faces (both in Cardigan Bay and at Plymouth) is probably due to the generally more intense surf action experienced on such aspects.

Both the upper and the lower limits of *L. pygmaea* are variable. On heavily splashed peaks it may persist to 2 ft. above E.H.W.S., on flatter shores it is rare above M.H.W.S. (These figures relate to Cardigan Bay only.) Its lower limit is difficult to fix with certainty, but it has been taken as low as M.L.W.N. - 0.5 ft. at Alltwen, which agrees with Cotton's (1912) observation that the lichen may extend to within a few feet of low water. Generally, however, it is infrequent below M.T.L., which appears to be its lower limit at Plymouth (Naylor, 1930). Grubb (1936) has taken it no lower than M.H.W.S. at Peveril Point. Usually, even on steep faces, *L. pygmaea* occurs most frequently and extensively between M.H.W.S. and E.H.W.N., i.e. within the Balanoid zone, a fact on which most workers are agreed.

*Lichina confinis*. This, like *L. pygmaea*, is poorly represented on the friable and unstable cliff face of the region, but occurs on peaks such as Craig y Fulfran. At Plymouth, Naylor (1930) assigns it a vertical zone of 2–3 ft. only, due to the generally low height of the cliff. Naylor, however, quotes Knowles as describing *L. confinis* to 50 ft. above high-water mark at Howth in Ireland, while Cotton (1912) gives it a 12–15 ft. range at Clare Island. The actual upper limit in Cardigan Bay has not been assessed with accuracy, but it was noted that the species extends to at least 15 ft. above E.H.W.S. on many peaks. Its lower level is normally about 4 ft. above M.H.W.S., and *L. confinis* does not accompany *L. pygmaea* into the intertidal zone.

### B. Fauna

*Barnacles*. Barnacles are the dominant intertidal animals over the stretch as a whole, and in most areas the midtidal region is occupied by a well-developed 'Balanoid zone'. Geographically, Cardigan Bay is intermediate between the Cornish Peninsula where *Chthamalus stellatus* is dominant (Fischer-Piette, 1933; Moore & Kitching, 1939), and the North Irish Sea where this species is absent or rare (Moore (1935*a*) at Port Erin) and *Balanus balanoides* is dominant. Both species occur freely in the Aberystwyth neighbourhood, and since it will be convenient to consider the Balanoid zone as a whole it is first necessary to distinguish the differences in distribution between the two species. *Chthamalus* is somewhat the less tolerant of shelter, as Kitching (1935) has shown to be general (though with some exceptions) in Argyllshire, and as Moore & Kitching (1939) have demonstrated experimentally. In Cardigan Bay this species is scarce or absent in protected areas near Borth, on College Rocks, and in other localities. *Chthamalus* is typically dominant on the upper shore, and has a higher upper limit than *Balanus*. The latter may reach E.H.W.S. in exposed positions, but *Chthamalus* exceeds this by 3 or 4 ft. in such places. Normally the upper limit of *Balanus* lies around M.H.W.N. as Moore (1935*a*) has described, while *Chthamalus* extends to M.H.W.S. as it does on the Argyllshire coast (Kitching, 1935). Whereas *Balanus* extends downwards to L.W.S., *Chthamalus* was not taken below M.L.W.N. in Cardigan Bay, and it is only occasional at this level. In Cornwall *Chthamalus* occupies the whole tidal range, and the Cardigan Bay data confirm Moore & Kitching's (1939) observation, that as adverse factors (lack of Atlantic water?) become more pronounced the tolerance of *Chthamalus* to immersion decreases, and its lower limit is raised. The height at which the change in barnacle population from *Chthamalus* to *Balanus* occurs is extremely variable. I have found surfaces with *Chthamalus* dominant as low as E.L.W.N., and patches of *Balanus* as high as M.H.W.N., but generally, over the whole area, *Balanus* tends to be dominant from just below E.H.W.N. downwards. Shelter may be important, but no direct effect can be traced; Moore & Kitching (1939) suggest a competition for food, and the writer would like to suggest that the time of spatfall (*Balanus* in spring and early summer, *Chthamalus* in winter) may be important also.

The Balanoid zone is excellently developed on the steepest and most exposed surfaces (e.g. peaks and reefs) and poorest on level sheltered shores such as College Rocks. Both surf and current favour barnacles, as Fischer-Piette (1929, 1936, etc.), Moore (1935*a*), Hatton (1938), and others have noted, the moving water providing transport of oxygen, food, waste products and larvae. Thus heavy encrustations may occur on surfaces sheltered from surf but washed by strong currents.

The texture of the substratum is undoubtedly of prime importance to the adult barnacle; smooth boulders and polished rock may carry thousands of young individuals and spat, but older individuals are confined to cracks and rough rock. In the Monk's Cave Region it is common to find exposed, but smooth, seaward-facing ledges bare of both fucoids (due to surf action) and adult barnacles (smooth surface). Spat, however, settling haphazard as it does, is often profuse on such ledges, and it would appear that older and larger barnacles, offering greater resistance to the waves (and to moving shingle), find greater difficulty in adhering to such a smooth surface. Cyprid larvae of *Balanus* settle and metamorphose in early summer, and it is probable that by the following winter their increased size and the incidence of winter gales combine to cause an enormous mortality in the population.

There is a marked negative correlation between barnacle and fucoid distribution, but the writer can observe no direct abrasion effect of fucoid fronds on the barnacle population such as Kitching (1935) describes. Under thick algae barnacles are generally poor, but do survive, and probably the screening efficiency of the algal fronds on suspended food is decreased by the high detritus content of the water of the Bay. Moore (1935*a*) records a similar state of things in the Tamar estuary, and suggests the same explanation. The effect of barnacle-covered rock in cutting and tearing algal fronds has already been mentioned.

Loose, shifting material is inhibitive to both *Chthamalus* and *Balanus*, because of its pounding and polishing effects on the rock, and normally barnacles are poorly represented on the cliff face and on the upper shore. Sometimes the presence of loose material results in the greatest concentration of barnacles being found on protected landward faces, rather than on exposed seaward faces, which is a reversal of the normal state of things.

The upper limit of the Balanoid zone is marked on steep exposed faces by a 'barnacle line' which is visible for some distance. This '*Chthamalus* line' (since *C. stellatus* is the dominant species at this level) varies in height according to the intensity of wave action, as the following examples demonstrate:

M.H.W.S.	on Twr Gwyllanod, and the seaward stanchions of the Pier.
M.H.W.S. - 1 ft.	on the south face of Craig y Fulfran.
M.H.W.N. + 1 ft.	on the Promenade wall behind Castle Reefs.
M.H.W.N.	on the east face of Twr Gwyllanod.

On more sheltered and level beaches the line is indistinguishable, but since the headlands and projections of the cliff extend fairly far seaward the line is obvious on such steep rocks and faces at most localities in the region, while it is also marked on breakwaters and on the Promenade Wall. This line marks the upper limit of barnacles in quantity (i.e. of the Balanoid zone), but *Chthamalus* normally extends a few feet further up in small patches; for instance, on the south-west corner of Twr Gwyllanod spots are found up to E.H.W.S. + 2 ft. Probably both desiccation and time available for feeding are effective influences in determining this limit; even so it is surprising to find plankton feeders such as barnacles at a height where they are never completely submerged and may be untouched by splash even for comparatively long periods.

The lower limit of barnacles is variable, but spots of *Balanus balanoides* have definitely been found as low as E.L.W.S. Moore (1935*a*) records the species to between M.L.W.N. and M.L.W.S. in the Isle of Man, but to E.L.W.S. in the River Yealm (Moore 1935*b*); Huntsman (1918) to below tide marks in Nova Scotia. The lower limit of barnacles in quantity depends on whether the lower beach has a good fucoid cover or not. Where steep reefs

occur and a zone of *Fucus serratus* is absent, a well-marked 'Balanus line' can often be observed. This may be as low as M.L.W.S. on a very exposed face such as the south-west corner of Twr Gwyllanod, at M.L.W.S. + 1 ft. on the pier stanchions, and in such places the zone beyond that of barnacles is dominated by encrusting algae. On gentler and rather less exposed slopes (e.g. Castle Reefs) this *Balanus* line may be as high up as M.L.W.N. - 1.5 ft., and below it *Sabellaria* is dominant. That the raising of the line is due to increasing shelter is evident on Twr Gwyllanod where, in a crack on the western face, the line shoots up over a foot above its height on the exposed surface, and descends again beyond the crack. Again, in a deep crevice on the southern face of the same rock *Sabellaria* is dominant from above M.L.W.N. downwards on the vertical sides of the cleft. The effect of surf in lowering the lower limit of *Balanus* is also noted by Moore (1935a). What exactly determines this lower limit is difficult to imagine. Competition with lithothamnium or with *Sabellaria* cannot account for it, since the barnacle zone sometimes passes directly downwards into an area of bare rock. As Moore (1935a) suggests, it may possibly be due to some ill-effect of immersion which is locally mitigated by the influence of surf in carrying downwards bubbles of air.

The occurrence of spat in localities which are obviously unfavourable to the adult barnacle has already been mentioned, and often spat may be observed to have settled both above and below the limits of the adult. Hatton & Fischer-Piette (1932), Moore (1935a) and Hatton (1938) all note this, and state that such individuals which settle outside the normal zone later succumb to the ill-effects of excessive air exposure or immersion.

*Sabellaria alveolata*. Fischer-Piette (1936) describes the ideal conditions for *Sabellaria* as follows: Sand for tube construction must be available; water movement must be sufficiently strong to cause active transport of food and sand, but not so strong as to expose the sand tubes to the danger of mechanical injury. Sand, suspended food and local shelter from surf are all available in Cardigan Bay and the species is generally well represented.

*Sabellaria* is more tolerant than the fucoid algae of surf action, but is less tolerant than the barnacles, and it is not at its best on steep faces unless these are protected (e.g. by overhangs, crevices, gulley banks, etc.). Where shelter is good, thick cushions are developed, and these are common on the northern edges of rocky stretches wherever these abut on fine sand, as at the Clarach end of the Constitution Hill Rocks, and the northern edge of the Wallog-Borth Rocks. In more exposed areas (e.g. Bath Rocks, the southern part of the Monk's Cave Region, etc.) *Sabellaria* is more local and the patches are less thick, but in many places a *Balanus-Sabellaria* zone may be described in mid-beach, with barnacles on the tops of the ledges and *Sabellaria* in the depressions. The tolerance exhibited by the polychaete to steep slopes increases at low-tide levels, and at M.L.W.S. the worm often forms fairly thick cushions both on flat exposed rocks and on vertical seaward-facing ledges, even though fucoids may be absent or very poorly developed and *Rhodymenia* or *Corallina* the dominant weed.

Loose material is harmful to the patches of worm tubes, unless the beach is sheltered and the shingle is not liable to much shifting. On such protected boulder beaches (e.g. Tanybwllch Boulder Beach) the worm may occur quite extensively.

The flora associated with cushions of *Sabellaria* has already been discussed; in addition, the polychaete worm *Eulalia viridis* commonly occurs in the tubes.

Along gulley banks and on flat rocks there is some evidence of a competition for space

between *Balanus* and *Sabellaria*. In such places, while water movement seems to be sufficiently strong to allow the development of a thick encrustation of barnacles, it is *Sabellaria* which is dominant. Cushions of the worm tubes frequently overlies previous barnacle areas, and it would appear that once surf action is sufficiently reduced to offer little chance of mechanical danger, then *Sabellaria* is able to colonize previous barnacle patches, and is dominant in the competition for space.

The upper limit of distribution on open rock lies around 9 ft. above C.D. (i.e. approximately E.H.W.N. - 1 ft.), but under thick weed cover (e.g. on College Rocks) *Sabellaria* is common above this level. It occurs down to below M.L.W.S., but generally dies out before E.L.W.S. and is very scanty at this level. Where wave action is very heavy and a rich zone of laminarians is present the worm may be absent between M.L.W.S. and E.L.W.S. (e.g. Castle Reefs).

*Osilinus lineatus*. Walton (1915*b*) records *Osilinus* south of Alltwn Headland only; he states that it disappears in the Aberystwyth region, which receives drainage from lime-free grits, and that it does not reappear further north until Towyn is reached. But John (1941) reports it on College Rocks and suggests that *Osilinus* is extending its range northwards. During the course of the present survey the animal has been taken along the entire stretch of coast from Twr Gwylanod to Borth; its distribution, however, is still curiously local. As far north as Tanybwlech *Osilinus* is very common in areas of both rock and boulders, but while the ground seems suitable at Castle Point no specimens were taken here, though on the neighbouring College Rocks it is fairly common, especially on a patch of larger pebbles under the pier. Bath Rocks again failed to yield a single specimen, but in the Constitution Hill Region the snail is fairly common (though not as frequent as it is south of Tanybwlech) except at the extreme Clarach end. It is very occasional at the Clarach end of the Clarach-Wallog Rocks, but increases towards Wallog Boulder Beach where it again occurs in fair numbers. Further north, in the neighbourhood of Craig yr Wylfa, *Osilinus* is almost as frequent as it is near Monk's Cave, but beyond this it dies out in numbers towards Borth. At first glance it would appear that the scarcity of *Osilinus* on rock which abuts on sandy beaches may be due to some harmful effect of fine sand; this suggestion is contradicted by the presence of large numbers of the snail on isolated boulders in extensive sandy patches near Monk's Cave. The reason for this local and sporadic distribution is difficult to imagine, but Walton's (1915*b*) suggestion that the lime-free drainage north of Alltwn is responsible is not substantiated by the present (1946) distribution of the organism.

*Osilinus* is definitely not fond of strong surf (as Fleure & Gettings (1907) also remark) and is not generally associated with dense concentrations of barnacles. Neither does it favour a thick cover of fucoids. The favourite habitats of the species are areas either of boulders or large shingle (especially in gulleys and watercourses), and smooth ledges polished by abrasion. Under such conditions (e.g. at Monk's Cave and Alltwn) *Osilinus* is frequently the only animal species present in numbers, limpets and barnacles being restricted to crevices in the smooth rock. Thus at the top of the shore, in many places, it is possible to distinguish an '*Osilinus* zone', often associated with *Enteromorpha compressa*.

Colman (1933) assigns to this species a very narrow vertical range of 2 ft., from just below M.H.W.N. to just below E.H.W.N. (these and all subsequent levels quoted from Colman's survey are corrected data, with no allowance made for splash). Both in Cardigan Bay and in localities near Plymouth (including Church Reef), however, though

*Osilinus* is characteristic of the top of the beach, the writer has found it quite commonly outside this range; Moore (1940) also records it from M.H.W.N. to M.L.W.N. at Wembury. Fleure & Gettings (1907) describe the snail at high-tide levels in Cardigan Bay, and during the present survey it was taken commonly up to M.H.W.N. + 1 ft. and occasionally under weed or on flat rocks off which water drains slowly up to M.H.W.S. The snail continues to be common down to M.T.L., and though it may show some signs of dying off just below this level, groups of *Osilinus* were taken as low as M.L.W.N. - 0.5 ft. (e.g. on Tanybwllch Boulder Beach). The lowest specimen recorded was found at 1.5 ft. below M.L.W.N. The lower limit is generally variable; thus on Wallog Boulder Beach, on areas near Cormorant Rock, etc., it does not appear to extend lower than E.L.W.N.

*Gibbula umbilicalis*. Walton (1915b) states that this species, like *Osilinus*, is absent from the lime-free drainage areas of Aberystwyth, and is restricted to the coast south of Alltwen. He records one colony just north of this headland, however, and suggests that *Gibbula* is extending its range northwards. This appears to be so, for during the present survey *G. umbilicalis* was taken commonly as far north as Borth. Like *Osilinus*, its distribution is local and sporadic and the distributions of both species are similar, though with the following exceptions: *Gibbula umbilicalis* is poorly represented on some parts of Morfa Boulder Beach where *Osilinus* is common, yet it is fairly frequent on Bath Rocks where *Osilinus* is unrecorded; north of Craig yr Wylfa *Gibbula umbilicalis* extends in greater numbers to Borth than does *Osilinus*. Both species are absent from Castle Rocks, and it appears that there may be some similarity both in the northward extension of the two forms since 1915 and in their present distributions.

This similarity extends to the types of habitat preferred by the snails, i.e. stony gulleys, boulder areas and flat rocks. *Gibbula umbilicalis*, however, is less common than *Osilinus* on bare polished ledges and is more tolerant of weed cover. It also appears to be slightly more tolerant than *Osilinus* of surf, and Fleure & Gettings (1907) attribute this to its lower shell height. But it is never common on very exposed reefs and generally shuns steep faces unless these are protected (e.g. gully banks).

The vertical distribution of *Gibbula umbilicalis* is lower than that of *Osilinus*. In Cardigan Bay it is definitely common considerably above the M.L.W.N.-M.L.W.S. region which Moore (1940) describes as its zone of abundance. In pools the species may be taken almost as high as M.H.W.S., but on open rock it does not occur above E.H.W.N. Under thick weed cover (e.g. on College Rocks), it may be fairly common at this level, but usually it is most frequent from E.H.W.N. - 1 ft. down. To just below M.T.L. *Gibbula umbilicalis* is generally common, and its lower limit appears to be influenced by local conditions. It is absent from the Laminarian zone at exposed points, but on sheltered boulder beaches (e.g. at Tanybwllch and Wallog) it has been taken as low as -0.5 ft. C.D. (i.e. M.L.W.S. - 0.7 ft.). No specimens were recorded at E.L.W.S. anywhere.

*Gibbula cineraria*. Walton records this as rare in Cardigan Bay in 1915, but during the present survey it was found fairly frequently in some localities, though never as commonly as *G. umbilicalis*. It favours similar ground to the latter species, but at a much lower level on the beach, and is best represented at low water on Morfa Boulder Beach, on parts of the Alltwen and Monk's Cave Rocks, etc. Where sand replaces rock or boulders at low tide, the species is absent (e.g. between Clarach and Borth), but where rock occurs *G. cineraria* was found as far north as Craig yr Wylfa.

Its lower limit lies beyond tide marks, and generally it does not extend into the littoral



zone higher than M.L.W.S. + 2 ft., though an occasional specimen was found as high as M.L.W.N. - 0.5 ft.

*Nucella lapillus*. In most places this is one of the most common gastropods on the shore, congregating in large numbers on barnacle-covered masses and boulders. Barnacles form its main article of diet according to Moore (1936*a*), and the relationship between the distribution of *Nucella* and that of barnacles is evident in Cardigan Bay as it is elsewhere. However, while the species is more tolerant of waves and surf than the Trochidae (possibly because of its shell shape and the position in which it lies on the rock), it still requires a certain amount of local shelter in barnacle areas. It is commonly found in crevices, along gully banks, on horizontal rock and on overhangs, but the greatest numbers are normally to be found on steep but sheltered landward or north-eastern faces of reefs, rock masses or large boulders. It is difficult to judge with certainty, but the writer would suggest that shade may play some part in the choice of such a habitat, especially at high levels; even in the case of boulders and reefs fairly protected from direct wave shock on their southern aspects, *Nucella* still tends to congregate in its largest numbers on the shady north faces. The species is not partial to thick fucoid cover, and though it does occur under *Asco-phyllum* (e.g. on College Rocks), where the weed is profuse, the snail is more or less restricted to protruding peaks and ledges, on which weed is scanty and *Balanus* is best also.

The upper limit of zonation lies around E.H.W.N., which agrees with Colman's (1933) and Fischer-Piette's (1936) findings, but which is rather higher than Moore (1936*a*) describes. On the landward faces of outer reefs and in crevices on exposed peaks *Nucella* may occur up to M.H.W.N., but this may be attributed to the effect of splash. The lower limit is variable; Moore (1938) says that, in the absence of *Mytilus* (the alternative diet to barnacles), *Nucella* may end at the lower limit of barnacles, but that E.L.W.S. is probably its normal lower limit though it may extend to a depth of 10 fathoms. In Cardigan Bay the species is occasional to E.L.W.S., and it may be common as low as M.L.W.S. where fucoids are poor and *Balanus* is plentiful. Where a thick zone of *Fucus* carpets the lower beach and *Balanus* is scanty, then *Nucella* may be poorly represented below the limit to which this *Fucus* zone extends up the shore. It was never found to be frequent below M.L.W.S. anywhere.

The colour of the shell is usually a greyish white (with a greenish tinge due to algal infection), less often a dirty yellow, and occasionally a bright orange. Moore (1936*a*) relates this yellow colour to some effect of surf. Mauve, pink or banded shells are related by the same worker to a preponderance of *Mytilus* in the diet. In the few places where mussels are common in this region (e.g. near Borth), no such coloured shells were taken and it appears that *Nucella* sticks to barnacles for food even where both these and *Mytilus* are available.

*Mytilus edulis*. Mussels are found occasionally along the whole stretch of coast, but are only abundant in a few small areas. One *Mytilus* area occurs on a small deposit of boulders near the harbour mouth at Aberystwyth. There are no such areas south of this to Twr Gwylanod, or north of it until Craig yr Wylfa is reached. On the rocky peaks of Craig yr Wylfa dense patches of *Mytilus* occur on the vertical sides up to E.H.W.N. and under conditions of extreme surf action, while low-tide reefs in the same area, exposed only at low spring tides, are also densely packed with mussels. Further north, on the level shore to Borth, the mid-beach is occupied by a *Balanus-Mytilus* community, and bunches of

mussels are also frequent on the wooden piles and breakwaters along the fine sandy beach of Borth. Fischer (1929) relates the distribution of *Mytilus* to factors of surf action and the presence of organic material in suspension. Both conditions would appear to be fulfilled in Cardigan Bay, and the restriction of mussels to a few areas only is puzzling.

*Littorina neritoides*. The habits and habitat of this species are discussed at length by Lysaght (1941), and many of her conclusions appear to be confirmed by the survey in Cardigan Bay. The snail is somewhat local here, generally poor on most of the cliff face, due to the presence of the shingle beach at its foot, and improves on headlands, peaks and rock masses lying outside the influence of loose material. It definitely favours rough and vertical faces, exposed to the south and south-west; and its restriction to northern and north-eastern faces as described by Walton (1915*b*) is not at all obvious. On sheltered areas (e.g. College Rocks, Wallog and Morfa Boulder Beaches, etc.) *L. neritoides* is extremely infrequent or absent, and it is poorly represented even on vertical aspects where these are sheltered by masses or peaks on the seaward side. On the southern, south-western and western faces of Twr Gwyllanod, for instance, the species occurs in amazing numbers, which are markedly reduced proceeding round to the northern and eastern faces. Exposure to wave action and rough vertical rocks, then, appear to be essential to *L. neritoides*.

The upper limit of distribution lies well above E.H.W.S., and is clearly affected by the amount and height to which splash and spray are experienced. Thus on the southern face of Twr Gwyllanod the snail is very common to 25 ft. above C.D. (i.e. E.H.W.S. + 10 ft.) at least, the difficulty of climbing the peak making it impossible to record its absolute upper limit; on the eastern or landward face, however, *L. neritoides* is occasional to E.H.W.S. + 4 ft. only. Down to about M.H.W.S. or a foot below this the snail is usually common, but below this it is occasional only and has to be looked for with care. It was taken (with young *L. rudis* and *L. littorea*) in empty barnacle shells and in cracks well down the beach, but its scarcity makes it difficult to define the true lower limit of the species. Specimens were recorded as low as M.L.W.N. - 1 ft.; Lysaght (1941) records it to below M.T.L. on Plymouth Breakwater, and states that sexually mature specimens have been taken on piles submerged for at least a year. Thus *L. neritoides* has a much wider vertical range than is usually described (Colman, 1933), and has an amazing range of tolerance to conditions of immersion and desiccation.

*Littorina rudis*. This prefers rather more sheltered conditions than *L. neritoides*, and is generally better on broken ledges and in boulder areas than it is on smooth or shallow-fissured faces; yet the species is intolerant of excessive furoid growth, and does not favour very sheltered areas. Gowanloch & Hayes (1926) describe the same type of habitat for the snail. Being less demanding with regard to surf and to rock slope, *L. rudis* is more common and less local than *L. neritoides* in its distribution in Cardigan Bay, and it is often one of the most characteristic species on the upper beach (e.g. on Tanybwllch Boulder Beach). Normally part of the *L. rudis* zone is absent, due to the presence of shingle, and the species appears to be less tolerant of moving material than *Osilinus*.

Moore (1940) describes a well-defined upper limit between M.H.W.N. and M.H.W.S., Fischer-Piette (1936) places it at a similar level, but Colman (1933) finds *Littorina rudis* common above E.H.W.S. at Wembury as it is in Cardigan Bay. Its upper limit lies below that of *L. neritoides*; on the southern face of Twr Gwyllanod *L. rudis* occurs only as high as E.H.W.S. + 7 ft., and is common only up to E.H.W.S. + 5 ft. In localities less subject to

splash this upper limit is lower, but generally lies in the E.H.W.S. region or just below this. The lower limit varies, but *L. rudis* definitely persists (usually as small individuals in empty barnacle shells, but occasionally as large individuals) as low as M.L.W.S. + 1 ft. Moore (1940) states that it may be abundant between M.L.W.N. and M.L.W.S. in some localities, but rare below E.L.W.N. in others; Gowanloch & Hayes (1926) describe its optimum zone as just above M.L.W.N. ('low-mid-tide'). Generally in Cardigan Bay *L. rudis* is abundant to about M.T.L. and dies out below this, though in places it may occur fairly commonly as low as M.L.W.N.

*Littorina littorea*. This again is somewhat local in its distribution, but does not seem to be related in distribution with the Trochidae as Walton (1915*b*) suggests. Like *Osilinus* and *Gibbula*, *Littorina littorea* frequents fairly sheltered and level ground or stony areas, and is often very common on low plateaux or in shallow pools. On steep faces, even protected ones, it is occasional only, and is less tolerant of surf than *Nucella*. *Littorina littorea* is often associated with cushions of *Sabellaria*, like *Gibbula umbilicalis*, especially in *Sabellaria*-fucoid communities. Another typical habitat is at the bases of isolated boulders on a sandy beach (e.g. near Monk's Cave). The general habit of periwinkles to congregate in large groups in shallow pools, on boulders, on isolated weed clumps, etc., is well marked.

The vertical distribution of *Littorina littorea* in the region is variable, and is influenced largely by local conditions of surf action, rock configuration and weed cover. The upper limit in quantity lies in the region of E.H.W.N. or a little below this, but occasional specimens may be taken as high as M.H.W.N. As Moore (1940) remarks, absence of weed from the upper beach may reduce the numbers of *L. littorea* above M.T.L. (e.g. Castle Rocks). Colman (1933) also records *L. littorea* to M.H.W.N., but Gowanloch & Hayes (1926) place the upper limit at M.T.L. (i.e. 'mid-mid-tide'); Rees (1934) remarks that 'the real home of the periwinkle is at low tide'. Moore (1940) describes a constant lower limit, the species being abundant at M.L.W.N. and less so at M.L.W.S., but this too varies in Cardigan Bay according to local conditions. On rocky beaches it is common only to just above M.L.W.N. (e.g. Bath Rocks), but on pebble beaches sheltered from surf *L. littorea* may be well represented as low as M.L.W.S. (e.g. Tanybwllch Boulder Beach, northern edge of College Rocks). The absolute lower limit in such localities is at least as low as E.L.W.S., though the species is not common below M.L.W.S. Colman (1933) records *L. littorea* to midway between M.L.W.N. and M.L.W.S., Moore (1936*b*) to E.L.W.S., and Huntsman (1918) to 20 fathoms in Nova Scotia. Hayes (1929) states that it can withstand immersion for 50 days. The absolute range of *L. littorea* in Cardigan Bay, then, would appear to be E.L.W.S. to M.H.W.N., with its zone of abundance varying according to local conditions between M.L.W.S. and E.H.W.N.

*Littorina littoralis*. Like the other Littorinidae, *L. littoralis* is local in its distribution, and this can be related to the distribution of fucoid algae. Where fucoids are poorly represented *L. littoralis* is occasional, but on College Rocks and on small fucoid areas elsewhere the snail is common. Apart from its indirect effect via the fucoid cover, wave action appears to be limiting directly, and it is rare to find *L. littorea* on plants or clumps of weed on exposed reefs.

The vertical zonation, too, is associated with that of the algae; where only the lower beach has a cover of fucoids then *L. littoralis* is also restricted to low levels, whereas on College Rocks it is abundant well above M.T.L. Moore (1940) and Orton (1929) give the upper limit as between M.T.L. and M.H.W.N., Gowanloch & Hayes (1926) as just below

H.W.N. ('high-mid-tide'), and Colman (1933) as just above M.H.W.N., i.e. slightly higher than that of *L. littorea*. In Cardigan Bay *L. littoralis* is often common among weed as high as M.H.W.N., and occasional to 1 ft. above this; in other places in the region it is only occasional at M.H.W.N. The lower limit is given as L.W.N. ('high-low-tide') by Gowanloch & Hayes (1926), as just above M.L.W.S. by Colman (1933), while Moore (1940) describes M.L.W.S. as its lower level of abundance. In the present survey it was never found commonly below M.L.W.N.-M.L.W.S. however rich the weed cover, and no specimens were taken below M.L.W.S., which appears to be the lower limit of *L. littoralis* in Cardigan Bay.

*Patella*. Three species of the genus occur in the region, *P. vulgata*, *P. depressa* and *P. athletica*. It is hoped to discuss the nomenclature, the identification, and the distribution of these in Cardigan Bay in a subsequent work; here their vertical zonation will be summarized briefly for purposes of discussion.

*Patella vulgata* L. E.L.W.S. to M.H.W.S. A decrease in numbers is evident below M.L.W.S., while on surf-beaten and shaded surfaces the species may occur to well above E.H.W.S.

*Patella depressa* Pennant (= *P. intermedia* Jeffreys). The upper limit in absence of splash is difficult to determine since the limpet occurs only on exposed rocks. On these it extends as high as M.H.W.N. and sometimes to M.H.W.S., but never as high as *P. vulgata*. It is common as low as M.L.W.S. + 1 ft., but dies out just above E.L.W.S.

*Patella athletica* Bean. Good from E.L.W.S. up to M.L.W.N., and to M.T.L. on very exposed low-tide reefs.

## VI. DISCUSSION

### A. General zonation

The presence of 'Littorina', 'Balanoid' and 'Laminarian' zones in Cardigan Bay may be recognized as the basic zonal pattern. This, as Stephenson (1939) suggests, is probably the fundamental scheme for the British coasts in general. In Cardigan Bay it is subject to modification according to variations in the rock formation and in the intensity of surf action. In its simplest form the pattern may best be seen on such exposed vertical faces as Twr Gwylanod, where it may be described as follows.

*Littorina* zone. *Littorina rudis* and *L. neritoides* are the typical inhabitants of a zone extending from just about M.H.W.S. (the height of the *Chthamalus* line) upwards. *Littorina neritoides* ascends to heights only occasionally reached by spray. Spots of *Chthamalus stellatus*, and a few *Patella vulgata* are present in the lower part of the zone, but the only plants are *Lichina confinis* in the upper part, with some patches of *L. pygmaea* and occasionally *Porphyra umbilicalis*, in the lower part. Where fresh water oozes out of the rock *Enteromorpha compressa* may also be found. Pools in the lower Littorina zone possess a growth of lithothamnia and some *Corallina*, together with *Patella vulgata*, *P. depressa* and *P. athletica*, but higher up these also disappear.

*Balanoid* zone. This extends from the upper limit of barnacles in quantity (i.e. the 'Chthamalus line', around M.H.W.S.) down to the beginning of the Laminarian zone which, too, is often marked by a lower barnacle line, the 'Balanus line'. *B. balanoides* is the dominant animal from just below E.H.W.N. downwards, *Chthamalus stellatus* above this. *Patella vulgata* occurs throughout, *P. athletica* is confined to the lower part, except in pools, and *P. depressa* is typical of the zone from M.H.W.N. downwards. *Littorina rudis* persists fairly commonly in the Balanoid zone down to about M.T.L., then dies out in numbers, while *L. neritoides* persists only as occasional individuals even from M.H.W.S.

down. *Mytilus edulis* may be characteristic of the zone in certain localities, and *Nucella lapillus* is common in cracks, on landward faces, and in other positions of local shelter. *Lichina pygmaea* occurs chiefly in the upper part of the barnacle belt, but is occasional lower down, and *Porphyra umbilicalis* is local.

**Laminarian zone.** This, like the other two, is characteristic of exposed points, where *Laminaria digitata* and *L. Cloustoni* are the dominant species. Weeds such as *Corallina*, *Fucus serratus*, *Gigartina stellata* and *Rhodymenia palmata* are common, while lithothamnium form extensive sheets over the rocks. The chief animal inhabitants are *Patella athletica*, *P. vulgata*, *Patina pellucida*, *Patelloida virginea*, etc., and occasionally *Mytilus* and *Nucella*.

This is the scheme found on very exposed points, and modification of this basic pattern is caused chiefly by increasing shelter. The Littorina zone is less well represented in sheltered areas, and *Pelvetia* appears at its lower level. In the Balanoid zone the effect of increasing shelter is to allow the development of weed, and where surf action is sufficiently reduced then barnacles are almost totally obscured by the fucoid series, *Fucus spiralis*, *Ascophyllum nodosum*, *Fucus vesiculosus* and *F. serratus*, as on College Rocks. With the advent of shelter; such animals as *Sabellaria alveolata*, *Littorina littorea*, *L. littoralis*, *Osilinus lineatus* and *Gibbula umbilicalis* also make their appearance. Between a state of affairs such as occurs on College Rocks and that prevailing at Twr Gwyllanod there exists, as has already been mentioned, a number of intermediate stages (see p. 284).

Rock configuration also has a profound effect on the basic scheme. Primarily it will interact with the factor of surf action, and where the shore is irregular the presence of peaks and ledges provides local shelter and allows local algal growth. The angle of the slope of the shore is also important in relation to wave action, and a typical Balanoid zone and Littorina zone are always best seen on vertical surfaces. Rock texture is also important both for barnacles and weed. Apart from these more general considerations there are two modifications of rock configuration which are characteristic of the portion of Cardigan Bay studied.

(1) Often the disappearance of rock and the presence of sand at low-water level eliminates the Laminarian zone completely.

(2) The presence of considerable quantities of loose material such as pebbles, boulders and shingle has a modifying effect. Normally, in the region, the cliff is footed by shingle; this is itself too unstable to support either plants or animals, and in addition it performs a scraping and polishing action both on the cliff face and on the upper shore rock. The Littorina zone is frequently eliminated by this factor, also the upper part of the Balanoid (or Fucoid) communities. In many places, where the boulders are large enough, a characteristic community of *Osilinus lineatus*, *Enteromorpha compressa* and *Porphyra umbilicalis* may occur, and these may be found even on the polished upper shore; or indeed lower down the beach in gulleys, etc.

Thus, though the basic pattern of zonation may be recognized in Cardigan Bay, it is rare to find it in all its simplicity, and the two chief modifying factors are local shelter from surf and the presence of loose material.

The general poverty of the fauna in the centre of Cardigan Bay has already been mentioned. Presumably the 200 species listed by Walton (1915a) and Horsman (1922) could be added to by careful and extensive observation, but still, the general impression gained of the shore here is that in comparison with localities visited in the Plymouth

neighbourhood, for instance, it is poorly populated. The writer is inclined to agree with Walton (1915*a*) that the factors of surf action, loose material and normally turbid water are important in this respect, especially the presence of so much shingle and sand combined with strong wave action. In addition, deep fissures and overhangs in which factors of surf and of desiccation are locally mitigated are not common, and on most shores these are normally rich in species. The geological nature of the rock is important in this respect; grits and shales weather into jagged reefs and flat surfaces, hollows and depressions such as occur in limestone, for instance, are not developed, and the characteristic fauna of such habitats is poorly represented. There seems no reason why local climatic conditions (which are typically cold north temperate) should prevent the existence of a rich fauna; neither is the salinity of the inshore waters in any way exceptional, except, perhaps, during periods of flood in the rivers. Even so, the rivers are comparatively small and their influence on salinity cannot be particularly marked except at their mouths, and the generally strong action of surf and waves tends to equilibrate the salinity. Thus the presence of loose pebbles, etc., the strength of the waves, the absence of very sheltered localities, and possibly the turbidity of the water are all probably responsible for the poverty of the intertidal zone in the centre of Cardigan Bay.

#### B. *The relation of species to tidal levels*

Fig. 8 summarizes the vertical zonations of the various species studied. In the case of such forms as barnacles, limpets and *Pelvetia*, an attempt has been made to reduce their upper limits to what they would probably be in the absence of splash which normally occurs on the cliff face where their upper limits lie. By comparing this with Fig. 7 and Table 2, it is possible to define approximately the percentage exposure to the air which the species can withstand, or which they find necessary. This has been done at Wembury by Colman (1933), and comparison with his results is interesting. (For purposes of comparison it is necessary, throughout this discussion, to convert Colman's levels and figures so that the 2 ft. splash allowance is deducted.) Table 3 compares the percentage exposure to the air for each species in Cardigan Bay with that at Church Reef.

Certain points are worth noting in this table.

(1) Generally speaking, the ranges I have described are wider than those given by Colman, probably as a result of the more extended nature of the present survey. This would explain the discrepancies for *Pelvetia*, *Fucus spiralis*, *Ascophyllum* (lower limit), *Laminaria digitata*, *Gigartina*, *Lichina*, *Balanus* (lower limit), *Osilinus*, *Nucella* (lower limit), *Littorina neritoides* (lower limit), *L. rudis* (lower limit), *L. littorea* (lower limit), and *Patella vulgata* (lower limit); and I have taken such species outside Colman's limits even on Church Reef itself.

(2) The lower limit of *Chthamalus* is lower at Wembury than it is in Cardigan Bay. The writer has personally confirmed this difference, finding the species definitely below the 20% exposure level at Wembury. The raising of the lower limit in Cardigan Bay has already been discussed (pp. 294–5).

(3) The upper limit of *Gibbula cineraria* is lower in Cardigan Bay than at Wembury, where I have taken it myself above 30% exposure. The comparatively infrequent occurrence of the species in the present locality may account for this discrepancy, or it may be that the species is nearing the northern limit of its distribution (since it appears to

be spreading northward since 1915), and is less tolerant of exposure to the air at this latitude.

(4) The upper limits of both *Littorina littorea* and *L. littoralis* are higher at Wembury; this too has been confirmed by personal observation. Possibly the general absence of a flat, fucoid-covered, upper beach in Cardigan Bay may account for this, for weeds at the top of the shore are generally confined to steep rock masses beyond the reach of shingle, and neither species is particularly tolerant of such conditions. Even so, it is strange that occasional specimens of these two snails are not found up to as high a level as they are at Wembury.

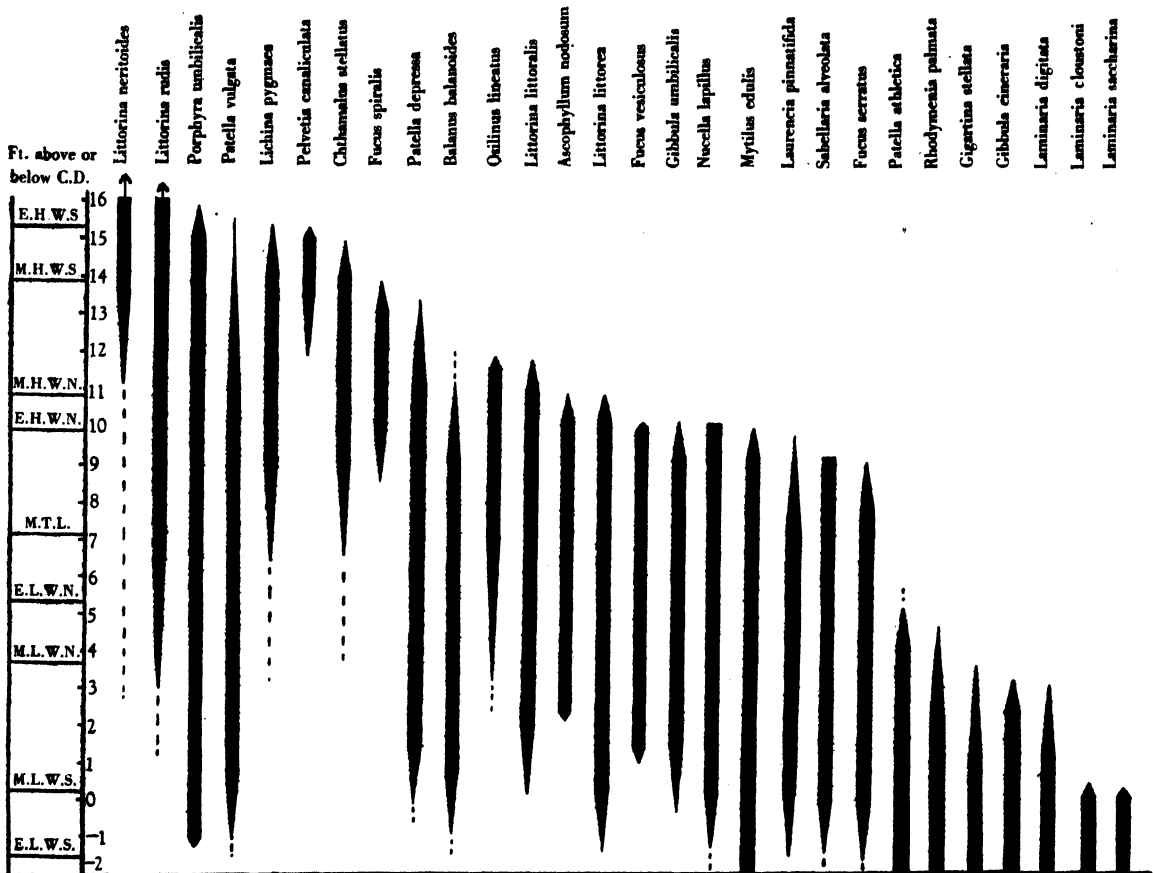


Fig. 8. Vertical zonation of plants and animals in Cardigan Bay.

Apart from these differences, there is a general similarity in the results which suggests that conditions do not change very drastically from South Devon to the Cardiganshire coast, and that the zonation of intertidal species in both localities is essentially the same.

### C. Critical levels

Colman (1933) considers three levels on Church Reef as being more 'critical' than others on the shore for the twenty-two species which he studied. Correcting these to predicted tide levels they are:

- (1) The lower limit of several intertidal species, at +0.5 ft. C.D., or just above M.H.W.S.
- (2) The upper limit of submarine species at +3.5 ft. C.D., or M.L.W.N. - 1 ft.
- (3) The upper limit of intertidal species at +12.5 ft. C.D., or just above M.H.W.N.

From Fig. 8 the number of upper and lower limits, and the total number of species occurring between +1 ft. and +4 ft., +2 ft. and +5 ft., etc., can be obtained as Colman (1933, p. 463) describes. These are given in Table 4, and from these figures the three graphs shown in Fig. 9 are constructed.

- (a) Number of lower limits.
- (b) Number of upper limits.
- (c) Total number of species present.

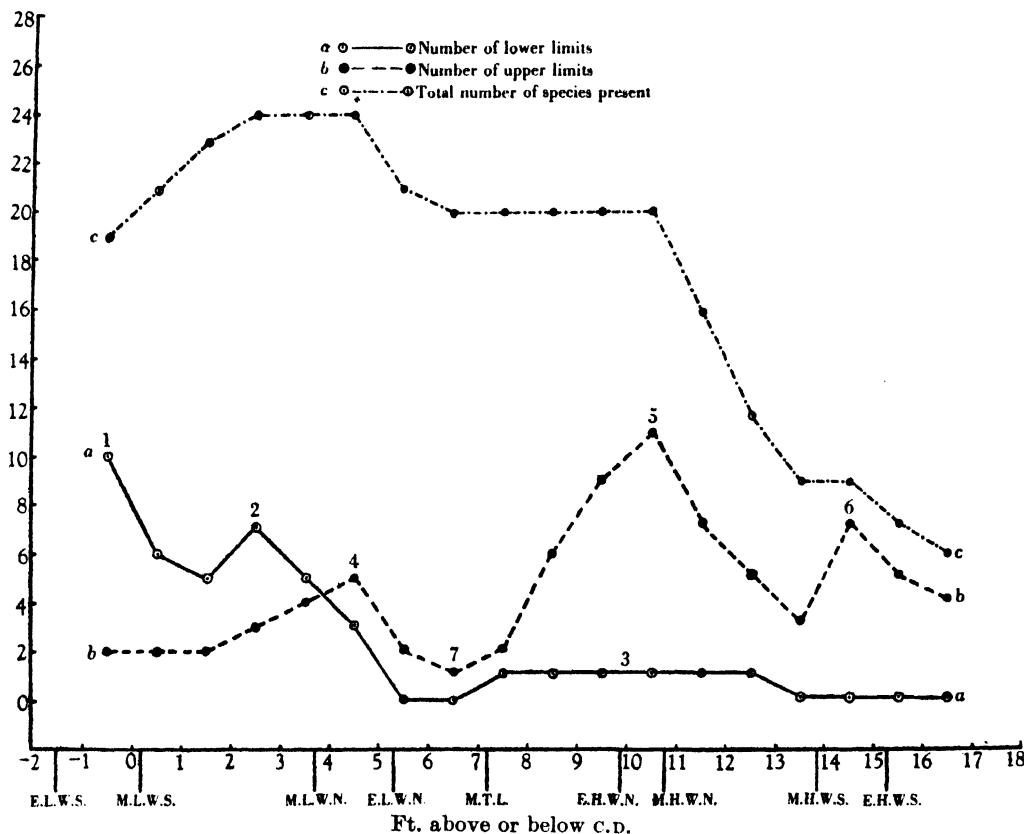


Fig. 9. Number of upper and lower limits and total number of species present at different shore levels. (For explanation see text.)

From these graphs the following points may be noted:

(1) The maximum number of lower limits lies between -2 ft. and +1 ft. C.D., i.e. between M.L.W.S. and E.L.W.S., at -0.5 ft. C.D. (This and all subsequent points are marked with the appropriate number in Fig. 9.) This apparently coincides with Colman's critical level of just above M.L.W.S., but is rather lower; however the two levels are identical in the sense that they mark, in both surveys, the lower limits of such species as *Balanus balanoides*, *Nucella lapillus*, *Patella vulgata*, *Gibbula umbilicalis*, *Littorina littorea* and *Fucus serratus*.

(2) A further, less well-marked maximum in the number of lower limits occurs between +1 ft. and +4 ft. C.D., i.e. at +2.5 ft. C.D., or between M.L.W.N. and M.L.W.S. This cannot be related with Colman's first level, which has already been related to (1). It is not cited by Colman, and does not appear on his graph (1933, Fig. 14, p. 465). In Cardigan Bay this level marks the lower limit of *Littorina rudis*, *L. neritoides*, and *Osilinus lineatus*, all of



which Colman records as ending higher up the shore. Furthermore, we have an additional species (*Fucus vesiculosus*) not considered by Colman, also ending here.

(3) There occurs a very vague and spread-out series of lower limits between +7 ft. and +13 ft. C.D., with its mean at +10 ft. C.D. or E.H.W.N. On Colman's graph, too, there is an upshore maximum of lower limits at E.H.W.N. -1 ft., more pronounced than mine, since he records *Osilinus lineatus*, *Littorina rudis*, and *Lichina pygmaea* as ending in this region.

(4) On the graph for the upper limits there is a small maximum, marking the upper limit of sublittoral species, between +2 ft. and +6 ft. C.D., i.e. at +4 ft. C.D. or just above M.L.W.N. This corresponds to Colman's second critical level of M.L.W.N. -1 ft.

(5) Another well-marked maximum of upper limits occurs between +9 ft. and +12 ft. C.D., i.e. at +10.5 ft. C.D., or just under M.H.W.N.

(6) A further maximum for upper limits is evident between +13 ft. and +16 ft. C.D., i.e. +14.5 ft. C.D., or midway between M.H.W.S. and E.H.W.S.

There are two peaks similar to (5) and (6) on Colman's graph, but he treats these as a single spread-out maximum to give his third critical level at just above M.H.W.N. From the Cardigan Bay graph (Fig. 9) it appears that these two peaks should be treated separately, and applying this to Colman's graph yields two critical levels, one at E.H.W.N., the other at M.H.W.S. -1 ft.

(7) The minima of the curves for both upper and lower limits coincide at about 6.5 ft. C.D., which is E.L.W.N. 1.2 ft. This is the least critical level on the shore for the species studied, and coincides with a level of E.H.W.N. -1 ft. at Wembury.

For convenience, these seven levels in Cardigan Bay and on Church Reef (according to Colman) are tabulated in Table 5. Comparing the two results, it will be seen that levels (3), (4), (5), (6) and (7) are all higher in reference to predicted tidal levels in Cardigan Bay than they are at Wembury, while level (1) is lower, and level (2) is unrepresented on Church Reef. In view of the fact that Colman worked only on the fairly sheltered landward portion of Church Reef it is possible that the raising of the five critical levels and the lowering of level (1) may be due, in part at least, to the greater intensity of wave action in Cardigan Bay. However, personal observation at Wembury has shown the writer that *Littorina neritoides*, *L. rudis*, *Osilinus lineatus*, and other species actually have a wider range on Church Reef than Colman's traverses indicated; consequently, for full comparison it is necessary to make a further analysis of the intertidal zonation in this locality. This study, together with a study of other localities near Plymouth, will be described later, and examined in relation to the Cardigan Bay results.

In the centre of Cardigan Bay, then, there appear to be five critical levels (the spread-out series of lower limits at E.H.W.N., i.e. level (3), cannot be regarded as critical) for the intertidal species studied. These are:

- |                                   |                                   |
|-----------------------------------|-----------------------------------|
| (1) Between M.L.W.S. and E.L.W.S. | (5) Just below M.H.W.N.           |
| (2) Between M.L.W.N. and M.L.W.S. | (6) Between M.H.W.S. and E.H.W.S. |
| (4) Just above M.L.W.N.           |                                   |

The least critical level is (7) E.L.W.N. +1.2 ft. These levels are indicated (with their appropriate numbers) on the graph showing percentage exposure to the air in Fig. 10.

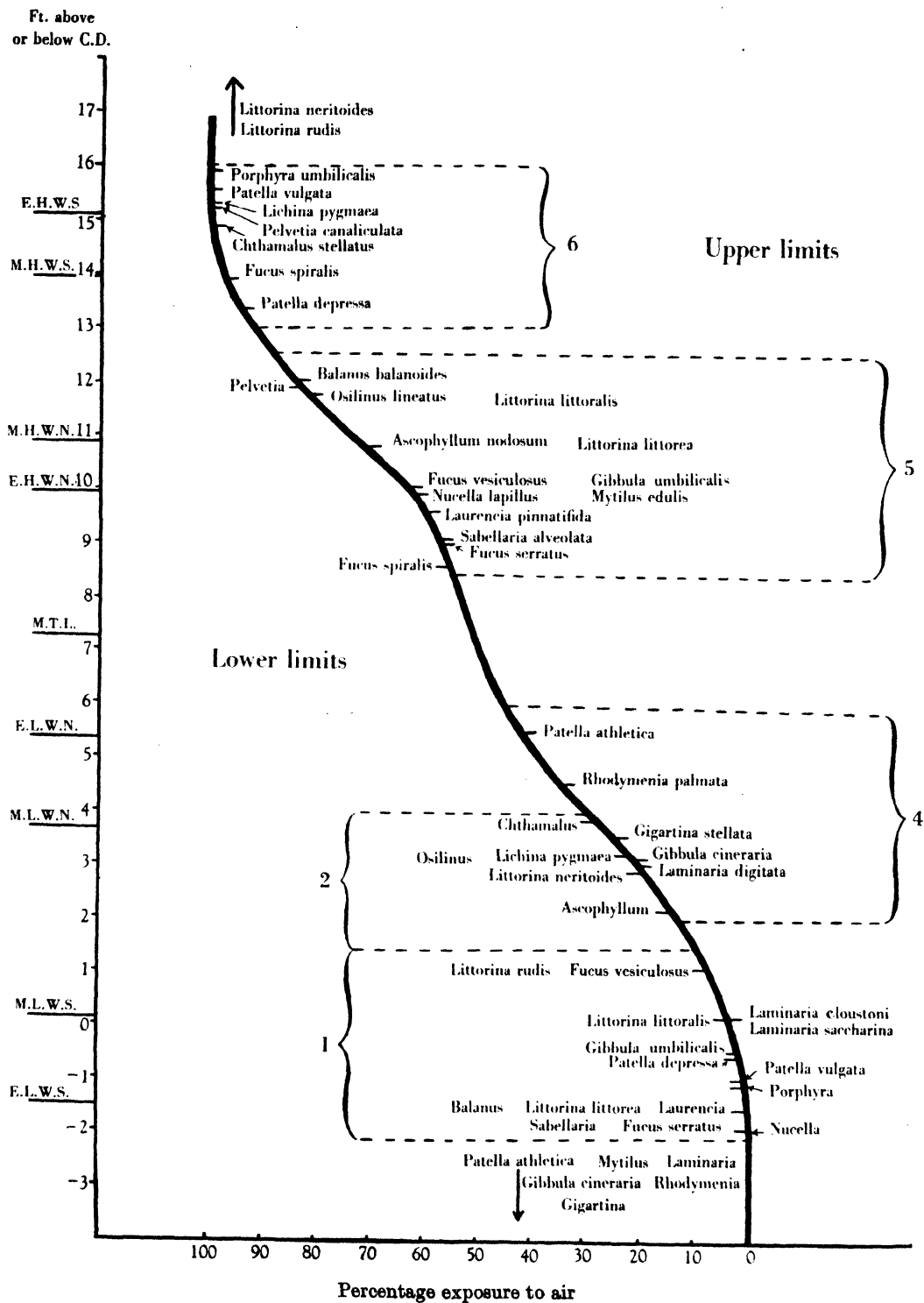


Fig. 10. Upper and lower limits of species plotted on the percentage exposure to air graph, to show the position of critical levels.

## VII. SUMMARY

1. A general description of the 10 miles of Cardigan Bay coastline included in the survey described is given, and tidal and climatic data for the region are discussed.
2. The percentage exposure to the air at different tidal levels is calculated.
3. A list of the species and localities studied is given, and the method of investigation is explained.
4. The general distribution of algae in the region is first discussed, after which the several plant and animal species selected for study are treated separately. For each species the horizontal and vertical distributions are described, and are compared with results obtained by other workers elsewhere.
5. The general features of zonation, the development of the Littorina, Balanoid and Laminarian zones, and the modifications of these by changes in degree of shelter and in rock configuration are described.
6. The percentage exposure to the air required or tolerated by the various species is considered, and the results are compared with those of Colman (1933). It is concluded that conditions in Cardigan Bay and at Wembury are essentially similar. Personal observation on Church Reef, Wembury, has given a more extended vertical range for many species than appears from Colman's traverses.
7. The concept of 'critical' levels is examined, and five levels are shown to be critical for the twenty-eight species studied in Cardigan Bay, i.e.
  - (a) Between M.L.W.S. and E.L.W.S.
  - (b) Between M.L.W.S. and M.L.W.N.
  - (c) Just above M.L.W.N.
  - (d) Just below M.H.W.N.
  - (e) Between M.H.W.S. and E.H.W.S.

The least critical level lies between M.T.L. and E.L.W.N.

These are compared with critical levels worked out by Colman (1933), and it is suggested that the greater exposure to wave action in Cardigan Bay may explain the differences, though it is also necessary to study Church Reef more extensively than was possible by the traverse method used by Colman.

The writer wishes to express his gratitude to Prof. T. A. Stephenson, who suggested the investigation, and under whose personal supervision the work was carried out.

Table 1. *Tidal scale for Aberystwyth*

	Ft. above or below c.d.
E.H.W.S.	+15.3
M.H.W.S.	+13.9
M.H.W.N.	+10.8
E. (lowest) H.W.N.	+ 9.9
M.T.L.	+ 7.2
O.D.	+ 7.1
E. (highest) L.W.N.	+ 5.3
M.L.W.N.	+ 3.7
M.L.W.S.	+ 0.2
E.L.W.S.	- 1.4

Table 2. *Percentage exposure to the air at different shore levels at Aberystwyth*

Ft. above or below c.d.	21 Jan.- 3 Feb. (max. 320) (a)	26 Feb.- 13 Mar. (max. 354) (b)	26 Apr.- 10 May (max. 353) (c)	21 Nov.- 5 Dec. (max. 353) (d)	Total for four periods (max. 1380) (e)	Percentage exposure (total for year $\times 100 \div 8760$ ) (f)
15	320	354	353	353	1380	100.0
14	320	339	340	353	1352	97.9
13	310	307	312	328	1257	91.0
12	292	281	287	293	1153	83.5
11	249	245	266	257	1017	73.7
10	207	212	221	228	868	63.0
9	188	198	207	202	795	57.6
8	169	187	196	183	735	53.3
7	157	176	185	168	686	49.7
6	144	163	169	150	626	45.4
5	120	145	153	124	542	39.3
4	85	121	125	88	419	30.4
3	53	92	96	47	288	20.9
2	27	68	70	16	181	13.1
1	7	49	39	0	95	6.9
0	0	27	29	0	56	4.0
-1	0	1	3	0	4	0.3
-2	0	0	0	0	0	0

Table 3. *Vertical zonations of species in terms of percentage exposure to the air in Cardigan Bay and Wembury (Colman, 1933)*

Species	Cardigan Bay		Wembury	
	Upper limit	Lower limit	Upper limit	Lower limit
<i>Ascophyllum nodosum</i>	71	15	75	30
<i>Balanus balanoides</i>	83	0	80	5
<i>Chthamalus stellatus</i>	100	28	100	20
<i>Fucus serratus</i>	56	0	60	0
<i>F. spiralis</i>	96	55	90	75
<i>F. vesiculosus</i>	63	8	—	—
<i>Gibbula cineraria</i>	21	0	40	0
<i>G. umbilicalis</i>	63	2	65	5
<i>Gigartina stellata</i>	26	0	20	0
<i>Laminaria cloustoni</i>	4	0	—	—
<i>L. digitata</i>	20	0	12	0
<i>L. saccharina</i>	4	0	—	—
<i>Laurencia pinnatifida</i>	60	0	—	—
<i>Lichina pygmaea</i>	100	22	97	52
<i>Littorina littoralis</i>	81	4	87	7
<i>L. littorea</i>	71	1	85	8
<i>L. neritoides</i>	100	20	100	90
<i>L. rudis</i>	100	8	100	60
<i>Mytilus edulis</i>	61	0	—	—
<i>Nucella lapillus</i>	62	0	65	8
<i>Osilinus lineatus</i>	82	22	75	60
<i>Patella athletica</i>	42	0	—	—
<i>P. depressa</i>	92	0	—	—
<i>P. vulgata</i>	100	0	98	12
<i>Pelvetia canaliculata</i>	100	87	98	86
<i>Porphyra umbilicalis</i>	100	0	—	—
<i>Rhodomenia palmata</i>	35	0	—	—
<i>Sabellaria alveolata</i>	57	0	—	—

Table 4. *Numbers of upper and lower limits and of total species at different shore levels*

Ft. above or below C.D.	No. of lower limits	No. of upper limits	Total no. of species
15 to 18	0	4	6
14 to 17	0	5	7
13 to 16	0	7	9
12 to 15	0	3	9
11 to 14	1	5	12
10 to 13	1	7	16
9 to 12	1	11	20
8 to 11	1	9	20
7 to 10	1	6	20
6 to 9	1	2	20
5 to 8	0	1	20
4 to 7	0	2	21
3 to 6	3	5	24
2 to 5	5	4	24
1 to 4	7	3	24
0 to 3	5	2	23
-1 to +2	6	2	21
-2 to +1	10	2	19

Table 5. *Critical levels in Cardigan Bay and on Church Reef, Wembury (Colman, 1933)*

Level	Cardigan Bay	Wembury
(1)	M.L.W.S. to E.L.W.S.	M.L.W.S. +
(2)	M.L.W.N. to M.L.W.S.	Not represented
(3)	E.H.W.N.	E.H.W.N. - 1 ft.
(4)	M.L.W.N. +	M.L.W.N. - 1 ft.
(5)	M.H.W.N. -	E.H.W.N.
(6)	M.H.W.S. to E.H.W.S.	M.H.W.S. - 1 ft.
(7)	E.L.W.N. + 1.2 ft.	E.L.W.N. + 1 ft.

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## BIOLOGICAL FLORA OF THE BRITISH ISLES

L.C. (Ed. 11) No. 2190

*Glyceria maxima* (Hartm.) Holmb.

J. M. LAMBERT

*Glyceria aquatica* (L.) Wahlberg, *Fl. Gothob.* 18 (1820); Smith, *Eng. Fl.* 1, 116 (1824); non J. & C. Presl, *Fl. Čech.* 25 (1819).

## Sect. HYDROPOA.

Known in Britain under a considerable variety of common names, usually as Reed or Water Meadow-grass, and Reed or Water Sweet-grass.

In parts of Norfolk is locally known as 'broad-leaf', and according to Miller & Skertchley (1878, p. 297) the terms 'lid' or 'white leed' were in common local usage in the Fens. Possible origin of latter word is of interest; writing of the Rolls of the Manor of Littleport (Cambs) of 1316-27, Marshall (1878, p. 107) states: 'The word "leyt" occurs a few times, and obviously meant a coarse sweet grass, what we still call "leed" (*Poa* (*Glyceria*) *aquatica*).' An extract from Bath Agricultural Papers (no date given) quoted by Sinclair (1816) states that in 'the Fens of the Isle of Ely... it is also called white lead, drying of a white colour'.

A stout, reed-like perennial grass, with an extensively creeping rhizome system bearing colourless scale-leaves when young and giving rise to initially erect leafy aerial shoots, those developing earliest in the year forming either vegetative or flowering culms, with later growth consisting of vegetative shoots only. Flowering culms up to 250 cm. long; first-formed vegetative shoots up to 200 cm. when fully developed, those produced later in the year correspondingly shorter. Tillers generally numerous, arising from bases of both flowering and vegetative shoots.

Leaves bright green, sometimes tinged with red when young, especially in the sheath; glabrous, with uniform longitudinal air-spaces interrupted by horizontal diaphragms; yellow or brownish triangle present at junction of blade and sheath. Sheaths entire for major part, distinctly keeled distally and broadly naviculate in cross-section. Blades up to 75 × 2 cm., linear, tapering very slightly to apex; upper surface very slightly ribbed (contrast prominent ribs of *G. fluitans* group) with apex of each rib lying above a lacuna and between the bundles, midrib excepted; epidermal cells of both surfaces often papillate; stomata numerous, small, not sunken, present as longitudinal lines on both sides of the blade. Ligule up to 6 mm. long, entire or slightly divided, truncate, but generally with an elongate central point. Auricles absent.

Panicle up to 45 cm. long, axis more or less scaberulous; branches angular, rough, arising in alternate clusters, with 4-5 unequal branches in lower clusters, and number decreasing progressively upwards.

Spikelets up to 12 mm. long, stalked, narrowly oblong and laterally compressed; pale green at first, later often overshot with brown or purple. Florets 3-12 per spikelet (generally 5 or 6); axis terminating in a very small undeveloped floret. Glumes unequal, lower 2-3 mm., upper 3-4 mm.; membranous, usually obtuse; generally 1-nerved, rarely with an indistinct lateral nerve; rough on margins, more or less scaberulous on keel, especially the upper glume. Lemmas 3-4 mm. long, not keeled, but with usually seven

very prominent and characteristic nerves; latter densely scaberulous on outside; awnless, apex membranous and generally nerveless, very obtuse or rounded. Paleas equal to lemmas or slightly shorter, boat-shaped, flanges scaberulous. Lodicules fairly large, more or less connate, though generally separable. Stamens 3; anthers up to 2 mm. long, yellow or purple. Styles 2, appearing to arise laterally; naked proximally, branched distally.

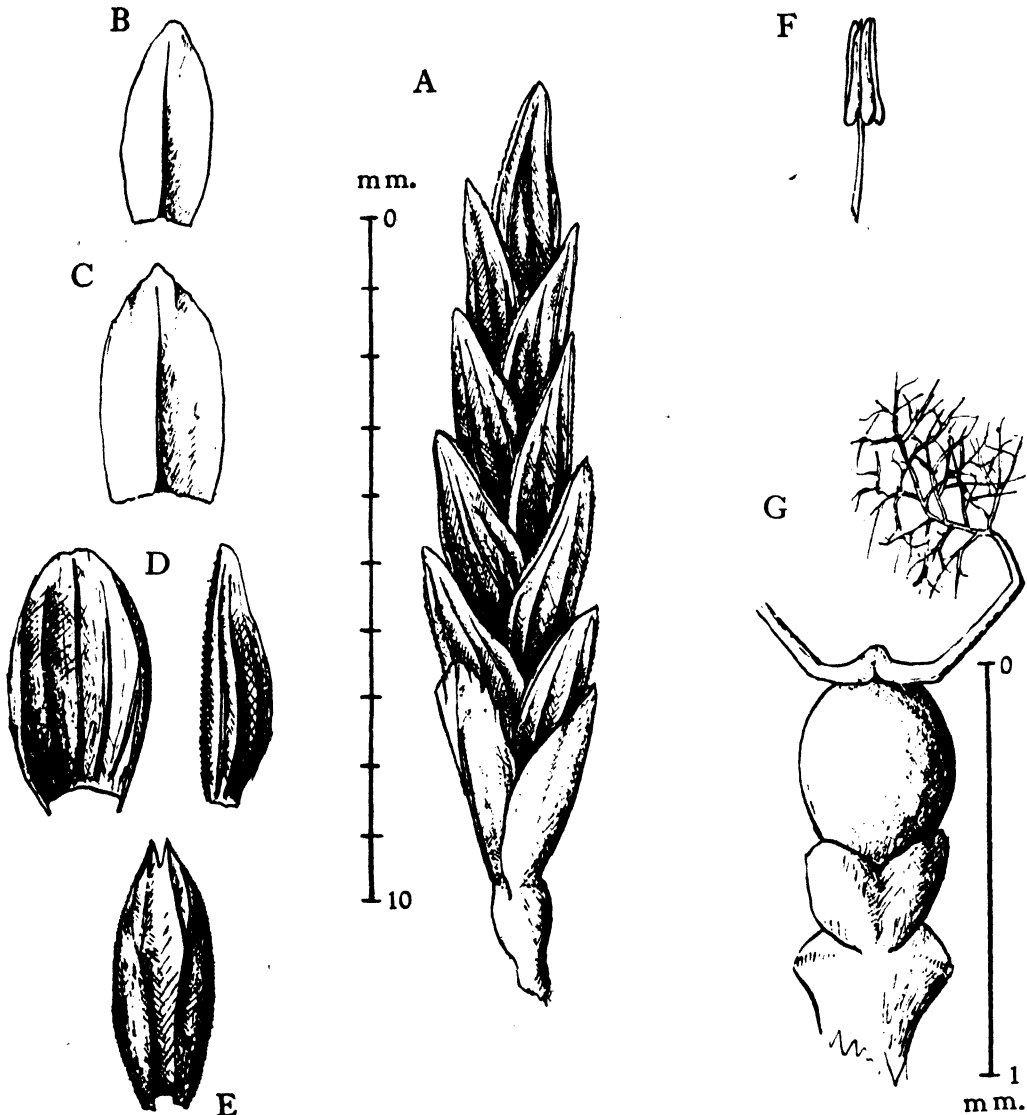


Fig. 1. Structure of the spikelet of *Glyceria maxima*. A, complete spikelet; B, outer glume; C, inner glume; D, palea (front and side views); E, lemma; F, anther (before anthesis); G, lodicules and ovary on axis. A-F all drawn to same scale; G further enlarged.

Caryopsis up to 1.8 mm. long, shortly stipitate, slightly flattened, dark brown when ripe, closely invested by palea and lemma when shed. Rachilla cylindrical and outstanding, somewhat enlarged at top (but less so than in *G. fluitans* group).

A distinct and well-marked species in Britain, generally regarded here as non-variable. Jansen & Wachter (1920), however, record a variety of forms from the Netherlands, the differences occurring chiefly in the structure of the panicle. Thus they distinguish: (a) var.



*typica* J. & W., with large panicle, stiff oblique branches, numerous spikelets, mostly 5–6 flowered (f. *multiflora* J. & W., with stiff thick panicle branches and 10–12 flowered spikelets, and f. *pauciflora* J. & W., with fine smooth branches and 3–4 flowered spikelets, are included as extremes within this); (b) var. *densiflora* Waisb., with dense panicle bearing short appressed branches; and (c) var. *umbrosa* Junge, with loose panicle bearing lax elongated branches. Junge (1912, p. 248) gives latter form as distributed in shady places, especially in swamps and woods, and constituting a transition towards var. *arundinacea* (see below).

Jansen & Wachter include all their forms with loose spreading panicles under *umbrosa*. Similar forms have received various names in the course of years; e.g. var. *laxiflora* Waisb., with panicles elongated and loose-flowered, and distal spikelets with very few flowers; var. *laxa* Noldecke, with panicle very spreading, almost hanging over (this variety given by Hegi (Fl. 1) as playing a prominent part in Danube and Baltic regions, where in some parts (especially in Hungary) it forms grass thickets); and var. *arundinacea* Aschs, with loose panicle, spikelets far apart, and smaller pales, which is probably a race from south-eastern Europe (Jansen & Wachter, 1920), possessing great systematic independence

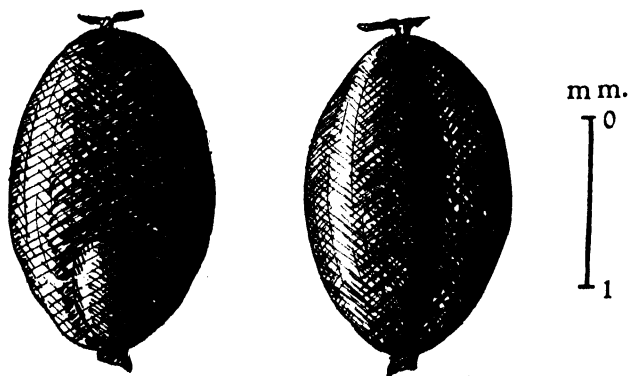


Fig. 2. Abaxial and adaxial views of naked grains of *Glyceria maxima*.

(Aschers. & Graebn. 2). It was given species status by Kunth, *Rév. Gram.* 1, 118 (1829), and, moreover, is ranked as a distinct species by Kelso (1934) in his key to *Glyceria* spp.\*

British material so far examined corresponds mainly to the *typica* of Jansen & Wachter, with extremes approximating to their forms *multiflora* and *pauciflora*; a few specimens could be related to the *umbrosa* type. In general, however, the distinguishing characters appear so indefinite, and transitional forms so numerous, that in absence of experimental evidence there appears to be no real basis for a taxonomic distinction between them.

A variegated form, with pale yellow-striped leaves, is in cultivation at Kew and elsewhere in the British Isles as an ornamental plant.

A riparian or paludal grass, with at least the roots in water or wet ground throughout the year; markedly basicolous, with high mineral requirements, and chiefly characteristic of rich alluvial soils of river valleys.

I. *Geographical and altitudinal distribution.* Present as an indigenous plant only in the North Temperate zone of Europe and Asia; recently introduced on a commercial scale through parts of Australasia, and thence to South Africa and possibly North America

\* The use of the trivial *arundinacea* for such a species is, however, invalidated by Dumortier's predated application of this name to the Linnean *Poa aquatica* (= *G. maxima*) itself (*Fl. Belg.*, 158 (1827)).

(see p. 315). Replaced as a native in North America by the closely allied *G. grandis*, S. Wats., and in China and Japan by *G. leptolepis* Ohwi.

(a) *Geographical distribution as an indigenous species.* (i) *British Isles.* Common to abundant throughout England except in the extreme south-west and towards the north. Previously known in the Isle of Wight (10) from one station only (Colwell Bay),

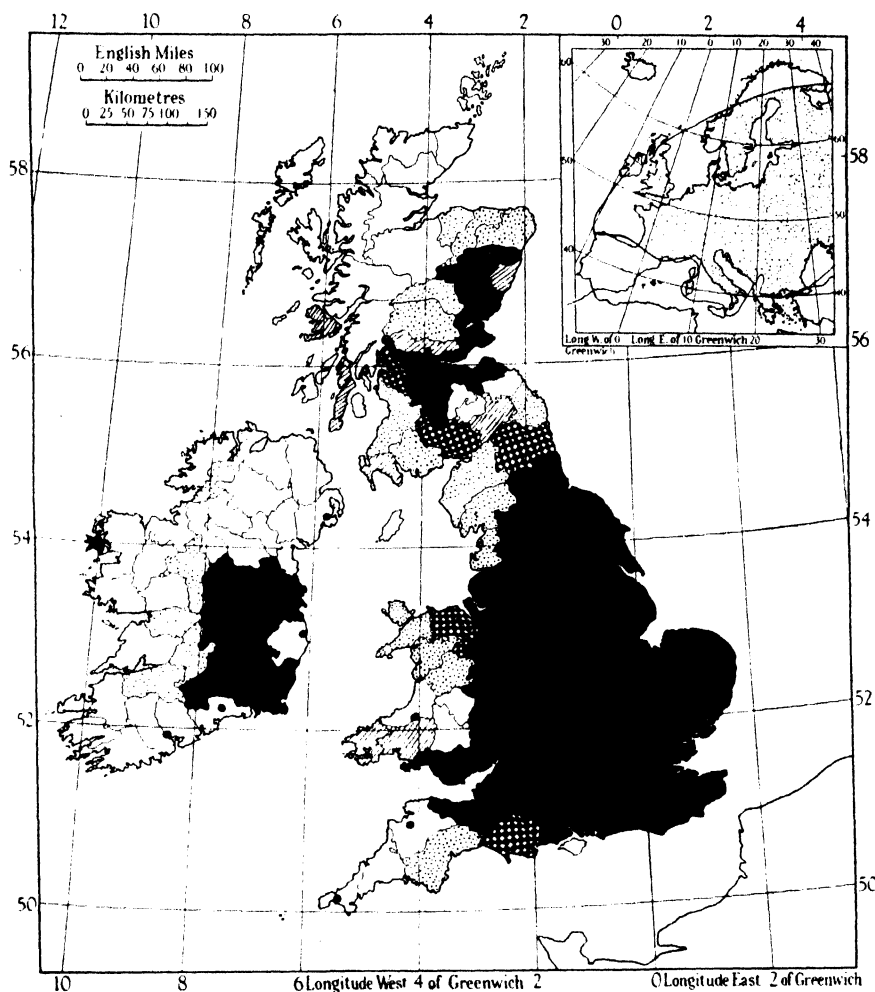


Fig. 3. *Glyceria maxima* (Hartm.) Holmb. Vice-comital distribution in the British Isles and (inset) limits of its distribution in Europe.

- Locally common to abundant.    ▨ Sparsely distributed.    ▩ Rare or very local.    □ Absent.  
 ▤ Recorded in *Top. Bot.* (or *Supplements*) and/or in *Comit. Fl.*, but no information as to abundance.  
 ● Isolated stations.    ★ Very probably originally introduced.

later reported as having disappeared completely from the Island (Stratton, 1913); rare in Devon and apparently absent from a large part of the county (Martin & Fraser, 1939), with only a single record for north Devon; one record only also from west Cornwall (1) (Davey, 1909), and a doubtful occurrence in east Cornwall (2), where original record by Keys (1872) was rejected by Briggs (1880); no record for the Scilly Isles.

In Wales, common only in Glamorganshire (41); distributed throughout Denbighshire (50), but occurring mainly in littoral regions in Flintshire (51) (A. A. Dallman); very local in Montgomeryshire (47), occurring abundantly along the Shropshire Union Canal in several places but apparently confined to it (A. E. Wade); absent in Breconshire and Radnorshire (42 and 43), and a single station only known in Cardiganshire (46) (Salter, 1935).

Rare in the greater part of Scotland and entirely absent north-west of Perthshire (87–9), south Aberdeenshire (92), Banffshire (94), and Moray (95), except for Mull (103) and Cautyre (101) (*Top. Bot. and Suppl. 1*). Towards its northern limits in Scotland occurs in some abundance in Clyde drainage area, and within Lanarkshire (77) has spread considerably eastwards along Forth and Clyde Canal within last 30–40 years (J. R. Lee, *in litt.* 1945). In south Aberdeenshire (92) recorded as probably originally introduced in a pond at Alford (Murray, 1836), from which point it subsequently colonized the major part of the Don as far as its mouth and appeared also in the Dee (though in less abundance) and at the mouths of burns which open into the sea some miles from the Don (*Trail Mem. Vol.* 1923).

In Ireland chiefly confined to the south-east and centre, where it appears clearly to be an invader (probably across an original land connexion) of the area now bounded by the south-east coast (R. L. Praeger). In general, southern limit formed by Suir basin (apart from two isolated stations in Cork (4–5) and Waterford (6)), and western limit by the Shannon. Its range in Ireland has been considerably extended since the eighteenth century by the making of the Grand and Royal Canals from Dublin to the Shannon, and the Shannon itself *may* have been colonized from these canals (R. L. Praeger); from Shannon, enters Ulster by way of Erne basin (Stewart & Corry, 1938), and there are two outlying northern stations in the south of Donegal (34) and Down (38). Believed to be non-native at its station on Achill Island, west Mayo (27), and also thought to have been originally introduced into Antrim (39), though no longer to be found there at its original station at Cranmore (Stewart & Corry, 1938).

Being ornamental, and very easily propagated by vegetative means, it is very possible that in certain counties from which there are only one or two isolated stations recorded, *Glyceria* may owe its presence to untraced artificial plantings (apart from those already noted). Since its effective reproduction is vegetative rather than by seed, this is especially likely when it occurs at a single station separated from neighbouring sources by stretches of high ground. F. Rilstone suggests this for west Cornwall, and Syme (1872) originally gave a similar suggestion for its most northern records in Scotland; moreover, Trail (1902) gives its occurrence in Banffshire, where it is confined to localities along the Deveron, as probably due to introduction (though giving no evidence of such). In general, it appears very doubtful whether this grass has yet reached its natural climatic limit in Britain; it is still apparently spreading northwards and westwards, the extent and rate being primarily determined by relative abundance and accessibility respectively of suitable aquatic habitats. This vegetative spread has been considerably aided in various parts (as noted specifically for Ireland) by the link-up of such habitats by artificially formed canals.

(ii) *Eurasia*. Generally distributed throughout North Temperate zone of Eurasia: but absent as a native from the corresponding zone of North America.

*Northern limits*. In Scandinavia, indigenous at least in Denmark, south Sweden and

east Finland; in other regions planted for fodder (chiefly during nineteenth century) and now completely naturalized in many parts and spreading rapidly; recorded as far north as Korpilombolo (lat. approx.  $66^{\circ} 50'$ ) in Sweden (Holmberg, 1926). Present in Karelia and south Lapland (Komarov, 1934) and distributed through Siberia south of the Arctic.

*Southern limits.* Generally regarded as absent from the Iberian Peninsula, but Merino (1909) records it from the neighbourhood of Santiago, Coruña; the numerous records given by Colmeiro (1889) are based on doubtful identification and therefore ignored. Absent from the Provençal and Maritime Alp districts of France and from Corsica (but present in Sardinia). Present throughout Italy, but rarer in south than in the north; recorded from Sicily. Distributed throughout the Balkan Peninsula except in Greece and Albania, and extending into Northern Transcaucasia.

(b) *Geographical distribution as an introduced species.* During last 20 years widely distributed on a commercial scale in Australasia by rootstock planting, the original source being a few plants grown in Victoria from introduced English seed (A. G. Brown, *in litt.* 1943, 1944); rapidly became established in Victoria, New South Wales and Tasmania (Anon. in *Queenslander*, 1930), where it proved vigorous enough to overcome indigenous swamp vegetation in suitable habitats (Audas, 1925). In New Zealand, recorded as having been successfully grown during the nineteenth century on an estate in North Island (Curl, 1879, p. 407), though there are some grounds for questioning the identity of the grass here referred to; Allan (1940) gives 1904 as date of first printed record of its occurrence. Distribution probably aided by commercial planting out during last 20 years, and is now established in various localities in North and South Island, being most frequent in Otago and Southland (Allan, 1940). In Thames Valley (North Island) has spread sufficiently to become an undesirably potent factor in blocking of waterways (Walker, 1946).

A limited number of planting experiments made in tropical Australia and New Guinea proved unsuccessful (Brown, 1929).

Introduced from Australia to a few places in South Africa, but limited planting experiments at stations in Natal, Pretoria, and Eastern Transvaal have indicated that *Glyceria* does not flourish or spread nearly as rapidly here as reported for Australia, the results being insufficiently promising to warrant further trials (L. Chippindale; J. P. Botha; J. D. Scott; all *in litt.* 1946).

In North America, establishment from imported seed so far unsuccessful, despite numerous trials (M. A. Hein, of U.S. Dep. Agric., *in litt.* 1945); no direct information available as to establishment from rootstock planting, but W. G. Dore (*in litt.* 1946) reports a number of very recent findings (earliest dated 1940) of stands of this species from stations in Ontario, Canada, suggesting at least three distinct introductions; it appears well distributed along roadside ditches in Lanark Co., indicating either establishment there for several years, or else rapid spread by seed (but cf., however, § VIII (g)).

(c) *Altitudinal distribution.* Typically a lowland species. In Britain, generally below 500 ft. (150 m.) (*Alt. range Br. Pl.*); range in Westmorland given as 200–700 ft. (60–210 m.) (Wilson, 1938). In Central Europe, hardly ever recorded above 500 m. (Aschers. & Graebn. 2).

Altitudinal limits probably determined more by mechanical and edaphic factors than by climatic considerations, since it is typically a grass of slow-flowing waters and rich alluvial substrates, and hence characteristic of the banks and flood-plains of rivers in their lower reaches.

II. *Habitats*. (1) *Types of habitat*. The following chief habitats may be recognized: (1) Banks of slow-flowing rivers and canals, with inorganic substratum; amount of water movement variable but never excessive. (2) Almost or completely stagnant ponds and dykes, with no marked inflow or outflow of water. (3) Ungrazed marshland in the flood-plains of rivers, with primarily inorganic soils of alluvial origin; generally flooded during at least part of the winter, but water table sinking below the surface in the summer. (4) The Broads and surrounding peat basins of the Yare Valley in Norfolk, with strongly tidal (though not brackish) water; here forming a prominent phase of the primary hydrarch succession, and occupying a broad zone consisting of a proximal entirely free-floating reedswamp portion which rises and falls with the tide, and a distal fen region which has less range of vertical movement owing to accumulation and compaction of peat below; forms definite societies also in the secondary anthropogenic fenland or 'mowing marsh', but limited to those parts of the fenland directly affected by the circulation of tidal water through the drainage system (Lambert, 1946).

(2) *Substratum*. Exhibits a considerable vertical range in relation to water level, occurring both as a reedswamp plant with roots and rhizomes immersed throughout the year (as in habitats (1) and (2) above), and also as a marsh or fen plant with the summer water-level well below the surface of the substrate (as in habitat (3) and the secondary fen regions in (4) above). Corresponds in this respect with *Phragmites communis* Trin., though when rooted in the substrate cannot extend as far into open water as the latter. Anchored *Glyceria* reedswamp can encroach on open water to a depth of some 60–80 cm. in absence of scour; extension of floating reedswamps of Yare Valley Broads into deep water theoretically unlimited, though in practice limits largely determined by tidal scour.

In fens and marshes, can maintain itself as a dominant in regions with summer water table sinking to some 50–60 cm. below surface in driest period. Intermittent readings taken during 1942–4 from a permanent water pit sunk in a dense secondary fen *Glycerietum* at Coldham Hall (Yare Valley) gave a range from +30 cm. (Jan. 1943) to –50 cm. (Aug. 1943).

In absence of competition, can apparently exist in much drier habitats. Sinclair (1816) gives the following: '...several experiments on this grass...prove that it may be cultivated on more elevated situations than has been supposed...', and D. Clouston (*in litt.* 1946) writes that it grew exceedingly well in loamy soil of his experimental grass plots (Aberdeen), though it produced only a few flowering heads (for effect of drought on flowering, see § V (c)). A small, stunted plant was found alive at Coldham Hall in very dry shallow soil attached to roots of prostrated willow, about 2 m. above general ground level; willow had been uprooted at least three years previously.

Certain Continental writers (e.g. Petersen, 1936, p. 220; Klapp, 1937, pp. 152–3) have stressed necessity for adequate supply of oxygen to subterranean organs for the maintenance of *Glyceria* in waterlogged habitats; observations made so far, however, indicate that air movement and oxygenation of substrate are not limiting factors in determining distribution of *Glyceria maxima*. In Yare Broads is a primary peat-forming plant in initial stages of hydrarch succession, and hence exists under reducing conditions conducive to formation of peat; substrate here gives off strong smell of hydrogen sulphide when disturbed, and summer diphenylamine tests (Pearsall & Mortimer, 1939) show uniformly negative reactions except for an occasional faintly positive reaction in upper 5 cm. (Lambert, 1946, p. 245). Moreover, frequently forms very vigorous communities in

completely stagnant water where water-level is maintained above substrate throughout the year (as in habitats of type (2)). Its abundance in regions with flowing water is probably far more related to mineral supply than to oxygenation of subterranean organs (see below).

Mature vegetative organs of plant are all aerenchymatous to greater or lesser extent; presence of higher internal concentration of oxygen in the roots than in surrounding medium is suggested by observations that immediate diphenylamine tests made on soil samples containing root fragments torn from living plants often showed distinct blue coloration in immediate vicinity of latter (especially towards broken ends) though no reaction could be seen throughout rest of sample. Moreover, Varley (1935, p. 30) reports that larvae of three species of insects were found piercing submerged roots of *Glyceria* with spine-like hind spiracles to obtain oxygen, thus suggesting fairly high concentration of latter in intercellular spaces.

Generally recognized to have very high mineral requirements (cf. Petersen, 1936, p. 220; Klapp, 1937, pp. 152-3; etc.); its high protein content (see § XI) may probably be regarded as an expression of this. In Scottish lochs is limited to those of lowland type, surrounded by rich agricultural land; especially luxuriant in Carlingwark Loch, which receives sewage from town (West, 1910). Able to maintain itself in stagnant water on rich inorganic soils, but on peat is confined to those regions where mineral supply is constantly renewed by moving water; hence abundant in fenland of Yare Valley in regions under the influence of moving tidal water, but absent from land-locked pools within the peat basins. Absent as a constituent of the hydrarch succession from the Broad of the other east Norfolk river valleys, where tidal movement is negligible or non-existent.

Selected Morgan tests (Morgan, 1941) made on some 24 soil samples taken at depths of from 0-20 cm. in three areas dominated by *Glyceria* in secondary Yare Valley fen at Coldham Hall gave medium to very high iron content throughout, with one exception; phosphate content also fairly high on the whole; nitrate nitrogen only present in any abundance in surface layers (cf. previous page), but considerable ammonia nitrogen present; calcium values variable, due partly to local inclusion of mollusc shells in samples. On the whole, values were greater in surface layers than farther down—this accords with suggestion of mineral supply renewed by flood water.

Though typically a fresh-water species, has been recorded from many stations which are brackish at least at certain times: e.g. by River Glaven, Norfolk (chloride content of ground water = 4.8 pro mille on 22 April 1946) and on sides of salt-water 'reens' at Whitewall Common, in Severn flats of Monmouthshire (River Lewis).

Can probably stand immersion for a short period in undiluted sea water, at least at non-active vegetative periods. An extensive patch, some 25 m. long, in a dyke draining reclaimed salt marshes between Cley and Kelling, Norfolk (normal chloride content about 0.6 pro mille), had subsequent growth apparently unaffected by immersion in full strength sea water (33 pro mille) during master tides of 28 March 1940; same patch, moreover, had obviously withstood more prolonged immersion during severe Norfolk sea floods of February 1938, though *Glyceria* was killed out in the more extensively flooded Horsey area (Ellis, 1938, p. 379) and not subsequently found in the affected area the following year (Ellis & Ellis, 1939, p. 39).

Trail's observations (*Trail Mem. Vol.* 1923) on spread of *Glyceria* in Aberdeen district, where it was reported as eventually reaching down to Don estuary and appearing in mouths of burns opening into sea some distance from the Don, suggests that marine

transport was involved (almost certainly of living detached vegetative portions, since reproduction by seed seems negligible); this may have required survival by propagating units of several days' or even weeks' immersion in sea water.

Appears to be limited to soils which are circum-neutral or alkaline in reaction; over 180 colorimetric readings from soil samples taken at various depths and at various periods of the year from different *Glyceria* habitats in Norfolk, Suffolk, Yorkshire and Oxfordshire have so far given a pH range of 6.6–8.4.

Able to colonize and flourish on essentially inorganic soils if mineral supply is adequate, but organic content of such soils is rapidly increased by subsequent annual accumulation of *Glyceria* debris, especially in waterlogged habitats where decomposition is retarded. A typical decrease in I/O ratio following colonization of an inorganic substrate by *Glyceria* shown by percentage loss on ignition values from the artificially formed lake at Blenheim Park, Oxfordshire, where an almost pure Glycerietum, some 8 acres in extent, occupies a deltaic area at the debouchment of the River Glyme; substrate of Glycerietum has been built up both by continuous silting from the Glyme itself and by accumulation of *Glyceria* debris (*Glyceria* having been a dominant colonizer throughout), and Table 1 shows a clearly marked inverse relationship between them with increasing depth of sample.

Table 1. *Percentage loss on ignition of soil samples from Glycerietum at Blenheim*

Depth of samples in cm.	% loss on ignition				
	1	2	3	4	5
0–5	63.5	61.6	64.7	59.7	68.7
5–10	46.8	32.9	49.9	30.2	48.0
10–15	32.9	36.6	28.6	30.9	33.4
15–20	24.1	29.9	14.9	22.4	23.4
20–25	22.3	22.5	20.2	24.9	21.3
25–30	17.8	—	20.3	17.0	—

Samples taken approximately 110 m. from water's edge and 30 m. from original bank of lake.

Approx. water-level on 1 May 1943 = +15 cm.

Approx. water-level on 12 July 1944 = –40 cm.

Tansley (*Br. Isl.* p. 630), writing of *Glyceria maxima* reedswamps of banks of rivers such as Upper Thames, states: 'During the winter the aerial shoots die, but do not dry out like those of *Phragmites*, and become compacted into a black slimy humus, the rotting mass from previous years forming the substratum of the current year's growth. Thus as growth proceeds outwards the portion of the mass nearest the bank is gradually raised. . . . Thus the growth of Glycerietum maximae depends much more on the accumulation of black humus produced by itself than on the trapping of silt. . . .' This, however, is not strictly the case for true reedswamp Glycerieta of river banks, exposed to some scour, since the coarse annual debris is so easily detached that it is washed away during the winter months before it is sufficiently compacted to remain in position; along banks of rivers with moderate current, silting factor seems predominant in building up of substrate within *Glyceria* reedswamps, though in older Glycerieta of hinder marsh regions removed from scour there is less silting and increased accumulation of *Glyceria* debris, and percentage loss on ignition correspondingly increases, as shown in Table 2.

In tidal Yare Broad, floating *Glyceria* reedswamp is protected in regions subject to scour by marginal fringe of anchored *Phragmites* (§ III (iv)), and debris sinking below floating raft is therefore retained; rise and fall of raft with tide prevents deposition of silt from above, and *Phragmites* fringe, where present, traps much of silt which would otherwise

percolate below: hence substrate below primary fen *Glycerietum* largely composed of loose straw-coloured raw *Glyceria* peat, with up to 85% loss on ignition. In secondary anthropogenic fens of Yare Valley, where occurrence of *Glyceria* on the mature compacted peat is limited to areas served by tidal drainage dykes (see p. 317), silt is freely deposited from above by flooding water from dykes; hence upper layers of substrate may have lower percentage loss on ignition than lower layers which were formed before dykes were cut (see Table 3).

Table 2. *Percentage loss on ignition for substrates of corresponding reedswamp and marsh Glycerieta*

	Marginal reedswamp areas: <i>Glyceria</i> growing in flowing river water	Marsh areas, lateral to main river: <i>Glycerietum</i> separated from river by bank of dredgings
Earlham region of R. Yare, Norfolk	23.48	45.81
Stoke-Shotesham region of R. Tas, Norfolk	26.55	38.81

Samples taken at depth of 5–10 cm.

Table 3. *Percentage loss on ignition at different depths in secondary fen Glycerietum at Coldham Hall, Norfolk*

Depth in cm.	Series 1	Series 2
0–5	63.0	56.3
5–10	56.3	47.2
10–15	74.7	45.5
15–20	75.3	53.3
20–25	78.2	81.4
25–30	84.7	84.1

If water and mineral salt supply is adequate, texture of substrate appears immaterial. Predominates on alluvial silt, but only because of other correlated factors; occurs on River Gravel and sand of Norwich Crag at edge of Surlingham peat basin; on slightly sandy soil which at one time formed bed of lake at Coate Water (J. D. Grose); on cinders in pond near coalmine at Rotherham, Yorks; on chalk covered with only a few cm. of silt at Earlham, Norfolk; on clay in old brick pit near Gloucester (J. W. & D. Haines), cf. also Sinclair (1816), 'on strong tenacious clay'; on peat in region of Yare Broad.

Recorded by Koopmans-Forstmann & Koopmans (1932) as occurring on sand, clay and silt in Friesland.

Australian introduced material found not to be particular as to texture of soil or subsoil (A. G. Brown).

Plants grown from tillers in boxes containing (a) gravel, (b) calcareous garden soil, and (c) local peat, sunk in secondary fen at Coldham Hall, Norfolk, showed no striking differences in growth after two years, except that root system was proportionally much more developed in gravel.

(3) *Other features of habitat.* (a) *Shade tolerance.* Generally found in fully exposed situations, but tolerant of slight shade. Growing vigorously as reedswamp on north side of overhanging riverside fringe of *Salix viminalis* in the Thames, near Oxford; dominant in parts under shade of *Salix alba* and *Betula pubescens* in wet woods on Tas flood-plain (Norfolk), but only in clearings among *Alnus glutinosa*, and noticeably less shade-tolerant than *Phalaris arundinacea*; in Blenheim Lake, Oxfordshire, very sparse under single



trees of *Acer pseudoplatanus* and *Ulmus campestris* overhanging from bank, but vigorous under *Salix fragilis*; in Norfolk Fens persists in non-flowering condition along drainage dykes in open *S. atrocinerea* carr, but generally absent from closed-canopy Alnetum glutinosae.

(b) *Resistance to scour*. Aerial shoots long and flaccid, outer ones often trailing over surface of water, and easily detached and torn away. Butcher (1933, p. 76) gives *Glyceria* as characteristically dominant only of the littoral stretches of rivers with current velocity of less than 500 yd. (457 m.) per hr.; according to Tansley (*Br. Isl.* p. 631), *Glyceria* is more resistant to scour than *Sparganium erectum* (but cf. § III, 1 (i)).

Floating *Glyceria* reedswamps of tidal Yare Broad very liable to disintegration by winter floods; this is so easily brought about that *Glyceria* can only maintain itself as primary encroaching agent in those parts of the Broad where tidal scour is at a minimum, unless protected by anchored *Phragmites* fringe (see § III 1 (iv)).

III. *Communities*. Generally forms a rather pure stand, sometimes dominating very extensive societies, with comparatively few subsidiary species; rarely occurs in subsidiary role itself to any other dominant, except in transition zones. Hence position occupied by *Glyceria* in relation to dominants of adjacent associated societies is first given for the different habitat types, followed by reference to subsidiary species occurring actually within Glycerieta of the different types.

(1) *Relation of Glyceria to dominants of adjacent societies*. (i) *River and canal banks, with slow-flowing water*. Forms definite zone in riparian community. Most constantly associated here with *Sparganium erectum* L.; when together, the two species show distinct zonation, with *Glyceria* occupying shallower water near the bank, but societies dominated by either species may follow each other in rapid succession along the course of a river, as noted by Butcher (1933) for East Anglian rivers. Tansley (*Br. Isl.*) mentions *Sparganium* as occurring within Glycerieta of the Thames, and competing successfully with them; in certain parts of the Thames below Oxford, *Acorus calamus* L. bears similar relation to *Glyceria*.

In Table 4, position occupied by *Glyceria* in riparian zonation is given for certain reaches of Upper Thames (Oxfordshire) and Upper Yare (Norfolk), and compared with that described by Steffen (1931, p. 301) for East Prussian rivers; the three lists show considerable similarity.

Table 4. *Position occupied by Glyceria maxima in riparian zonation of certain rivers*

Zone no.	Upper Thames, near Oxford	Upper Yare, near Earlham, Norfolk	General for East Prussian rivers (after Steffen)
1	Submerged types	Submerged types	Submerged types
2	<i>Nuphar luteum</i>	<i>Nuphar luteum</i>	<i>Nuphar luteum</i> , <i>Nymphaea alba</i>
3	<i>Scirpus lacustris</i>	—	<i>Scirpus lacustris</i>
4	<i>Phragmites communis</i> (often absent—if present, zone poorly developed)	<i>Phragmites communis</i> (often absent—if present, zone poorly developed)	<i>Phragmites communis</i>
5	—	<i>Sagittaria sagittifolia</i>	—
6	<i>Sparganium erectum</i>	<i>Sparganium erectum</i>	<i>Sparganium ramosum</i> (? = <i>erectum</i> ) included in preceding and succeeding zones as subsidiary species, but not given as forming definite zone in itself
7	<b><i>Glyceria maxima</i></b>	<b><i>Glyceria maxima</i></b>	<b><i>Glyceria aquatica</i></b> (= <i>G. maxima</i> )
8	<i>Phalaris arundinacea</i>	<i>Phalaris arundinacea</i>	<i>Phalaris arundinacea</i> —as for <i>Sparganium</i>
9	<i>Carex riparia</i> , <i>C. acutiformis</i>	<i>Carex acutiformis</i> , <i>C. riparia</i>	Mixed Magnocaricetum with <i>Carex acutiformis</i> most constant and with greatest degree of dominance
10	Mowing meadow	Raised bank of dredgings, with <i>Urtica dioica</i> and <i>Epilobium hirsutum</i>	'Rasenzone'

(ii) *Ponds, dykes, small lakes, and other water areas with almost still water.* In primary colonization of small ponds, *Glyceria* may often occupy whole or part of littoral area completely to exclusion of other prominent reedswamp species (cf. Area 6 of Table 5); in larger areas, inner zone to *Glyceria* dominated by a variety of species, but especially by *Sparganium erectum* (cf. Area 5, and to a less extent Area 8), or by *Equisetum fluviatile* (cf. West (1910) for Black Loch, Kirkcudbrightshire); J. L. Harper gives *Glyceria* as following on zone of *Carex vesicaria* in Stanford Reservoir, near Rugby.

Most constant associate at upper limit of Glycerieta of open-water areas is again *Phalaris arundinacea*, though former may be followed directly by species of *Magnocaricetum*; Nováček (1936), describing Glycerieta maximae in ponds near Třebíč, Moravia, gives species of *Magnocaricetum* as replacing receding Glycerieta when water-level is lowered during dry years.

(iii) *Marshes, with predominantly inorganic soils and summer water-level below surface of substrate.* When present forms a very dense community, generally with no other serious competitor in wetter parts, but with *Phalaris arundinacea* almost invariably becoming co-dominant or dominant with rise in level (cf. Weber, 1928, p. 40, for Germany); *Urtica dioica* may form small dense societies at still slightly higher levels.

(iv) *The peat basins of the Yare Valley in Norfolk.* In primary encroachment on open water here, probable that competitive reedswamp species of similar ecological requirements to those of *Glyceria* are largely limited or excluded by the peculiar mechanical conditions of the habitat, where a diurnal tidal rise and fall of 20–30 cm. is combined with a loose, shifting substrate, preventing anchorage by all species except those with deep-seated rhizomes. *Glyceria* is more easily adapted to these conditions than many of its competitors by its ability to form dense free-floating mats (Lambert, 1947*a*). Where scour is considerable, outer margin of floating Glycerietum is generally protected by a thin fringe of deeply anchored *Phragmites*, maintained there by purely physical factors of the habitat, but overwhelmed by *Glyceria* from behind as it advances into open water; farther back, *Glyceria* is in its turn replaced by *Phragmites* (of a more stunted growth habit than that of the marginal fringe), and here the dominance of *Phragmites* over *Glyceria* is thought to have a physiological rather than a physical basis and to be probably related to a decrease in available minerals in the hinder region of the fen (Lambert, 1946). The same physiological relation between *Phragmites* and *Glyceria* is seen also in the secondary anthropogenic fen regions, where *Glyceria* is limited to the sides of dykes which are served by circulating tidal water, while *Phragmites* (or *Juncus subnodulosus* in frequently mown regions) occupies the centres of the peat strips.

The reedswamp and marsh dominants in direct competition with *Glyceria* in its various habitats may be roughly classified into two types:

(a) Those which, like *Sparganium erectum*, *Carex riparia*, *Acorus calamus*, *Phalaris arundinacea*, etc., have similar nutritional requirements to those of *Glyceria*, but whose distribution in relation to the latter is largely determined by water-level.

(b) Those which, like *Phragmites communis*, have a similar vertical range in relation to water-level, but have somewhat differing physiological requirements in other respects.

(2) *The subsidiary species of the Glycerieta.* Subsidiary species listed from within limits of Glycerieta of selected areas covering the four habitat types are set out in Table 5; species given by Steffen (1931, p. 304) for East Prussian river valleys are included for comparative purposes. Lists show that whereas total number of associated species over



Table 5 (continued)

[illegible]



the whole range of habitats is large, actual abundance of individual species is in most cases low; moreover, only thirteen species are listed from 50% or over of the areas (in order of constancy, these species are *Phalaris arundinacea*, *Epilobium hirsutum*, *Solanum dulcamara*, *Urtica dioica*, *Filipendula ulmaria*, *Ranunculus repens*, *Carex acutiformis*, *C. riparia*, *Polygonum persicaria*, *Rumex conglomeratus*, *Lythrum salicaria*, *Phragmites communis*, *Lemna minor*).

Associated species are observed to occur in their greatest number and with greatest abundance in river-bank Glycerieta, where proximity of flowing water affords an effective method of dispersal of propagules, and where the *Glyceria* stands themselves are frequently open and disintegrated allowing for their establishment; moreover, here the total vertical range of *Glyceria* is encompassed within a very small area, so that subsidiary species from all levels are included.

IV. *Response to biotic factors.* Long recognized both in this country and abroad as a nutritious fodder crop (§ XI), and bears frequent mowing well. Records for both Britain (e.g. Curtis, 1777; Deakin, 1871; etc.) and for the Continent (e.g. Lecoq, 1844) show that in the past *Glyceria* was cut as much as thrice in one season. Tolerance of cutting shown by *Glyceria* may be correlated with its considerable tillering power.

In anthropogenic fenland of Yare Valley, *Glyceria* is maintained against competing *Phragmites* by regular summer cutting, while relaxation of such cutting allows encroachment by *Phragmites* except in immediate vicinity of tidal dykes; since *Glyceria* attains vegetative maturity earlier in season than *Phragmites*, early summer cutting would be expected to favour former to a greater degree than late cutting. *Glyceria* crops used for fodder are generally cut early in year, before emergence of panicle, while those destined for litter are cut any time up to September.

Readily palatable to stock in young fresh condition, and according to Clark & Malte (1913) can be closely pastured by horses and cattle; a commercial pamphlet issued by Law, Somner Pty. (date unknown) concerning Australian material also gives *Glyceria* as improved by trampling and close feeding, and Walker (1946) instances a New Zealand stand which can carry an average of a grown bullock per acre throughout the year, with necessity of doubling rate of stocking for much of the time in order to hold the growth. In Norfolk, however, *Glyceria* tends to disappear from drier grazing marshes (being replaced by smaller pasture grasses), while persisting in adjacent and similar marshes not accessible to stock.

Edges of floating reedswamps in Yare Broads frequently nibbled by geese, in some places so intensively that encroachment on open water is brought to a standstill. *Glyceria* of Yare Broads is also considerably damaged in places by feeding activities of wild populations of coypu (*Myocastor coypus* Mol.) which have become established there in considerable numbers from farm escapes.

Brown (1929) states that trampling will not damage *Glyceria* stands when well established. The vegetative stems are easily broken, but since detached or prostrated units root easily at the nodes, light trampling may aid vegetative propagation.

Because of high mineral requirements, stands of *Glyceria* are especially favoured by application of manure. In Britain, *Glyceria* is now rarely sufficiently valued as fodder crop for such manuring to be carried out, but on the Continent supplementary manuring is frequently suggested as a means of maintaining profitable stands (e.g. Weber, 1928).

V. (a) *Gregariousness*. Highly gregarious, owing to nature of vegetative reproduction; often forming very dense and extensive continuous stands.

A 1 m. square quadrat in dense secondary fen *Glycerietum* at Coldham Hall, Norfolk (examined Aug. 1943), contained 19 flowering shoots, 203 long vegetative shoots (of which 38 were affected with *Ustilago longissima* and may have been incipient flowering shoots), and 275 short tillers.

(b) *Performance in various habitats*. Other factors being equal, *Glyceria* reaches best development, both vegetatively and in production of flowering stems, in regions where summer water table is approximately at substrate level.

When growing among other tall reedswamp species, such as *Phragmites* or *Typha*, *Glyceria* may produce excessively long vegetative stems, held erect by surrounding vegetation, but incapable of supporting their own weight when isolated. Five vegetative stems of *Glyceria* growing among dense *Typha latifolia* at Wheatfen, August 1941, had an average length of 2.10 m. (range 1.88–2.22 m.), while the average of twelve stems from adjacent pure *Glycerietum* was 1.3 m. (range 0.8–1.9 m.).

(c) *Effect of frost, drought, etc.* Superficial examination has revealed no apparent damage by frost to any part of the plant during the last seven years (which period has included some severe winters).

An early summer drought, concomitant with excessive sinking of the water table, may inhibit development of inflorescences in potential flowering shoots. At Blenheim, Oxfordshire, where normally inflorescences developed to maturity in all parts of the marsh, the hot, dry summer of 1944 produced a definite reduction in inflorescence development with increasing height of the substrate; normal inflorescences were produced in the outermost reedswamp region, while with a rise in level of 50 cm. no external signs of an inflorescence could be found, though dissection revealed a small withered rudiment; transitional stages were found at intermediate marsh levels (Lambert, 1947*b*).

VI. (a), (b) *Morphology, etc.* Possesses a fairly superficial rhizome system generally limited to upper 10–15 cm. of substrate. A good general description is given by Raunkiaer (1895–9, p. 567): ‘The shining white, hollow runners, which may be half a metre long, are 5–7 mm. thick; they begin with 1–2 shorter internodes, after which follow a few much lengthened internodes, up to 10 cm. long or longer; after which the internodes, near the place of bending, become shorter and shorter, and the ascending shoot portion consists of several, quite short internodes after which follows the perpendicular leaf-bearing portion of shoot. Where the runners are sunk deep in mud, or where the plant grows in deep water, the ascending portion of the shoot has, however, frequently extended internodes. . . . From the points of attachment of the leaves of the part of the runner with extended internodes arise secondary roots; the largest number of roots is, however, developed from the points of attachment of the leaves at the place of bending, and from this part also new side shoots arise. The lowest side shoots have the longest runner portion; the higher the side shoot is situated on the mother shoot, the shorter is in general its runner portion, and the topmost buds form as a rule no runner portion at all but grow out directly to upright leafy shoots, which develop intravaginally, if the sheath has not already withered; the other side shoots on the contrary develop extravaginally’ (trans.).\*

\* This translation was made by the Imperial Bureau of Pastures and Forage Crops, Aberystwyth, who gave considerable help with abstracts and translations of Continental references.

Rhizome is covered when young with sheathing scale leaves, which soon disintegrate. Lateral buds of extended horizontal part of the rhizome generally remain dormant; only in one specimen of the many examined has a well-developed branch rhizome been found to arise from this region.

Adventitious root system dimorphic, consisting of (a) thick, white, generally unbranched roots, arising mainly from the bases of the erect stems at transition region from rhizome, and descending vertically to a depth of up to 60 cm.; and (b) more slender, shorter, whitish or brownish roots, bearing laterals of the first order only, arising from any or all nodes of the rhizome system, and spreading horizontally or obliquely in the upper 20 cm. of the substrate. Former type probably anchoring in function, latter mainly absorptive; transitional types between the two are often found. Root hairs appear to be produced only by those roots not immersed in water.

*Glyceria* reedswamps differ considerably in general physiognomy, probably mainly due to differences in mechanical substrate conditions (Lambert, 1947a). In all descriptive literature consulted, *Glyceria* is invariably recorded as erect in habit, though Armstrong (1917) notes tendency for stems to creep and root at the nodes. Typical erect stands occur on firm substrates, but in open-water areas with a loose basal ooze, natural buoyancy of the plant is too great for anchorage afforded, so that part or whole of *Glycerietum* forms a floating raft, with the vegetative stems showing marked tendency to overbalance and become prostrate at early stage of growth as a concomitant of lack of basal support; such prostration aids in general buoyancy and stability of raft, and production of tillers along prostrated stems aids in vegetative growth. *Glyceria* is better adapted morphologically than many of its competitors to the formation of floating rafts when substrate conditions necessitate it; hence it is able to exist under habitat conditions mechanically unsuitable for other superficially rooted reedswamp dominants with otherwise similar ecological requirements, but with a more rigid growth habit.

(c) *Mycorrhiza*. None definitely recognized in preliminary investigations.

(d) *Perennation*. Rhizome hemicryptophyte. Main branches of sympodial vegetative system become progressively less well developed towards autumn, with reduction both in length of rhizome portion and in height of aerial shoots; last-formed shoot generation of growing season, generally produced by early November, remains throughout winter with apical meristem at substrate level, protected by 3-4 persistent green leaves; activity of this meristem renewed in March to produce vigorous erect vegetative or flowering shoot, the renewal of apical growth being accompanied by a considerable increase in diameter of the newly formed portion of the stem over the older perennating portion.

In erect stands, aerial portions of the main vegetative and flowering shoots die off by November, not remaining upright as in *Phragmites*, but forming a dense and compact slimy mass over surface of substrate. On the other hand, in floating reedswamps, prostrate or inclined shoots of all ages remain green throughout winter; though older leaves at the base of shoots may decay, younger leaves of upturned tips of prostrate shoots persist to the following year. New spring growth may be initiated from both apical and lateral meristems of these perennating prostrate shoots, as well as from the rhizome system itself. Ability of prostrate shoots to overwinter, in contrast to autumnal death of erect shoots, may probably be correlated with their close proximity to or immersion in water, and to their sheltered position in relation to wind exposure; similar shoots artificially held erect, e.g. by the branches of a tree, die off in autumn in the usual way.



(e) *Vegetative reproduction.* Very rapid spread by underground runners owing to considerable number of successive shoot-generations formed in any one year; Syme (1872) quotes an example of the colonization of an area in the bed of an old pond of 30 sq.yd. (25 sq.m.) in 3 years from a single planted rootstock. Field observations suggest that in Britain up to five main shoot-generations (excluding short tillers) may be formed in one year; Raunkiaer (1895-9, p. 567) gives up to three shoot-generations as formed in each growing period, though suggesting that shoot development in general takes place twice a year (Danish material).

In floating reedswamps, the trailing immersed vegetative shoots represent an important factor in rate of encroachment on open water; nodal adventitious roots are produced abundantly along their whole length, with corresponding outgrowth of lateral buds, many of which form robust secondary shoots. When such secondary shoots are produced near tips of original parent shoots, rate of encroachment of the advancing fringe of the reed-swamp is far greater than if new advance shoots arose only from the rhizome system of more limited dimensions.

Where floating reedswamps are developed in areas with a certain amount of water movement, as in the Yare Broads, marginal masses of varying size (locally known as 'hover') are very readily detached and form floating islands, sometimes as much as 200 sq.m. in extent; similar floating *Glyceria* rafts are recorded from New Zealand (Walker, 1946). Size and abundance of these free-floating hover masses makes them very effective propagating units; smaller units, consisting often of isolated shoots or groups of tillers, are often detached from anchored river reedswamps, and are also effective in the capture of new habitats.

(f) *Longevity.* Individual rhizomes and roots appear to remain functional for one year only, the growth of subsequent years being carried on by newly formed vegetative organs.

(g) *Age at first flowering.* Observations in the field and with pot experiments indicate that seedlings probably do not flower until at least their second year.

(h) *Frequency of seed production.* Probably every year, but only in small quantities (cf. § VIII (g)).

(i) *Ecotypes.* No definite information, but see p. 312.

(j) *Chromosomes.* Considerable discrepancy exists between earlier and recent work. Avdulov (1928) gives 56 as the somatic complement for synonym *G. spectabilis*, while Stählin (1929) gives a similar number for *G. aquatica* var. *typica* and 28 for var. *arundinacea* (see p. 312). On the other hand, counts by Fitzpatrick (1946) on two specimens from Oxfordshire, and by G. L. Church (*in litt.* 1944) on material from Ontario (see p. 315), suggest that  $2n=60$ ; owing to technical difficulties, no absolutely satisfactory count has yet been made, but the number of 60 is supported by correlation of morphological and cytological characters with other related species of *Glyceria* (Church, 1942, and *in litt.* 1944) and by Maude's (*Mert. Cat.* and 1940) and Fitzpatrick's (1946) findings of somatic complements in multiples of 10 for other British *Glycerias*.

(k) *Physiological data.* Rouschal (1941) has shown for *Glyceria* that only strongly developed longitudinal veins serve for long-distance conduction of water; these alternate with weaker longitudinal veins, with fewer and narrower vessels, which are supplied by way of transverse veins from principal nerves, and distribute water for a short distance only. Measurements of water conduction in fully and half-grown leaves show that subdimensioning of conducting surface in basal embryonal zone of the latter represents an

internal limiting factor in their water relations, where, in contrast to mature leaves, the total quantity of water that can be conducted is used up in transpiration; rates of water conduction under experimental conditions are given as 3–5 m. per hr. for excised fully grown leaves, compared with 0.572 m. per hr. for basal embryonal region of half-grown leaves.

VII. *Phenology* (observations mainly from Norfolk material, 1939–46). (a), (b) Production of new roots—from bases of perennating shoots—generally begins in March; maximum development of roots from each shoot-generation occurs when apical meristem of aerial part of shoot is a few cm. above substrate level.

Appearance of new roots followed by an obvious and rapid development of leafy aerial stems from perennating shoots; outgrowth of new rhizomes from basal nodes of these shoots generally begins in early April and continues from subsequent shoot-generations until September or October.

(c) Majority of flowering haulms produced by leading shoots of first spring growth; inflorescences are sometimes, but more rarely, produced from the second shoot-generation of the year.

Upon dissection, inflorescence rudiments can be distinguished from vegetative meristems by end of April; panicles emerge from sheathing leaves about mid-June, with anthesis commencing early July; flowering period generally completed by mid-August, though isolated, poorly developed inflorescences have been found opening in September.

Great majority of British references consulted give July and August, or else July alone, as flowering period; Preston (1888) gives June to September or October for Wiltshire, with 21 June as average date, and 11 June 1870 as earliest observed date, for opening of first florets.

(d) Caryopses ripen 3–4 weeks after flowering (cf. Weber, 1928, Germany—4 weeks), and the majority are shed shortly afterwards; very few found still *in situ* by November.

(e) A small proportion of caryopses germinate immediately upon shedding, others not until after a resting period. In September 1943, 200 grains collected and sown immediately on cleared patch of fenland at Coldham Hall gave 11% germination in 14 days (subsequent results not obtained). At Blenheim Park, Oxfordshire, a few seedlings were found in October 1943 in open patches of the marsh, but had disappeared by the following spring; a larger number of seedlings, at varied stages of development, were observed in subsequent July on bare mud patches exposed by exceptional lowering of the water-level during prolonged summer drought.

Results of scattered preliminary laboratory experiments are given in Table 6. These indicate that a period of at least 6 months is probably necessary for maturation of most grains when stored dry under laboratory conditions.

Graphs plotted for various samples (see Fig. 4) sown after 6 months' laboratory storage show that under warm laboratory conditions maximum germination takes place during first 4 weeks after sowing. Caryopses collected from Coldham Hall in August 1941 and sown in the following May on range of nine natural soils at a temperature of 23–25° C. gave 79% average germination (range 70–90%) within 21 days of sowing. In *Technische Vorschriften für die Prüfung von Saatgut* (1928, p. 32), the *Keimschnelligkeit* (equated by Lehmann & Aichele (1931) to 'preliminary count' of *Rules for Seed Testing* (1927) is given as 7 days, and the *Keimfähigkeit* ('final count' of *R.S.T.* above) as 21 days.

Weber (1928, Germany) gives germination as occurring best under a shallow covering of water or in saturated soil (according to his observations under natural conditions and

Table 6. *Progressive germination of Glyceria maxima grains under laboratory conditions*

Year of exp.	Locality of sample	Temp. of germ. ° C.	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
1943-4	Blenheim Lake, Oxon	18-25	Lying on ← ground		C/S 2	—	—	—	46	(rest of grains then became fungoid)				
1941-2	Coldham Hall, Norfolk	23-25	C	Stored dry in lab.		→ S		—	—	40	—	(Exp. stopped)		
1945-6	Marsh by R. Tas, Norfolk	19-22	C	Stored dry in lab.		→ S		—	—	—	—	45	2	2
1941-2	Coldham Hall, Norfolk	23-25	C	Stored dry in lab.		→ S			60	15	—	(Exp. stopped)		
1943-4	Coldham Hall, Norfolk	18-25	C	Stored dry in lab.		→ S			22	28	—	(Exp. stopped)		
1943-4	Blenheim Lake, Oxon	18-25	C	Stored dry in lab.		→ S			2	42	—	(Exp. stopped)		
1943-4	Marsh by Kennington Lane, Oxford	18-25	—	C	Stored dry in lab.		→ S		—	40	—	(Exp. stopped)		
1945-6	Marsh by R. Tas, Norfolk	19-22	C	Stored dry in lab.		→ S			72	14	—	(Exp. stopped)		
1945-6	Marsh by R. Tas, Norfolk	19-22	C	Stored dry in lab.		→ S			78	(Exp. stopped)				

Upper row for each sample = months of collection (C), storage, and sowing (S).

Lower row for each sample = percentage germination each month after sowing.

with germination trials); preliminary laboratory tests with Norfolk material indicate that germination takes place equally well under 40 cm. water as on damp filter paper.

VIII. (a) *Mode of pollination*. Anemophilous, with typical mode of anthesis of those members of the family with well-developed lodicules; anthers and stigmas ripening together.

Godron (1873, p. 37, French material) gives 5 a.m. as average time and 15° C. as minimum temperature for '*une floraison abondante*'. Knuth (*Poll.* 3, 527) states 'anthers dehisce between 5 and 6 p.m. (probably for the second time)'. In Norfolk and Oxfordshire material, anthesis observed at varying times between 3 and 6.30 p.m. (G.M.T.); early

morning opening not yet actually observed, but material examined later in morning has shown every sign of recent anthesis.

A certain proportion of pollen appears infertile; in count of 208 grains from material from Sandford (Oxon) in July 1944, 20.6% grains were empty.

(b) *Insect visitors*. Occasionally hover flies, such as *Melanostoma mellinum* L., are found to be held by the proboscis between the glumes of florets which have closed rapidly after anthesis; such visitors may be either pollen-devouring (cf. Knuth, *Poll.* 3, p. 517) or attracted by the large glistening lodicules of the expanded florets (Knuth, *Poll.* 3, p. 516).

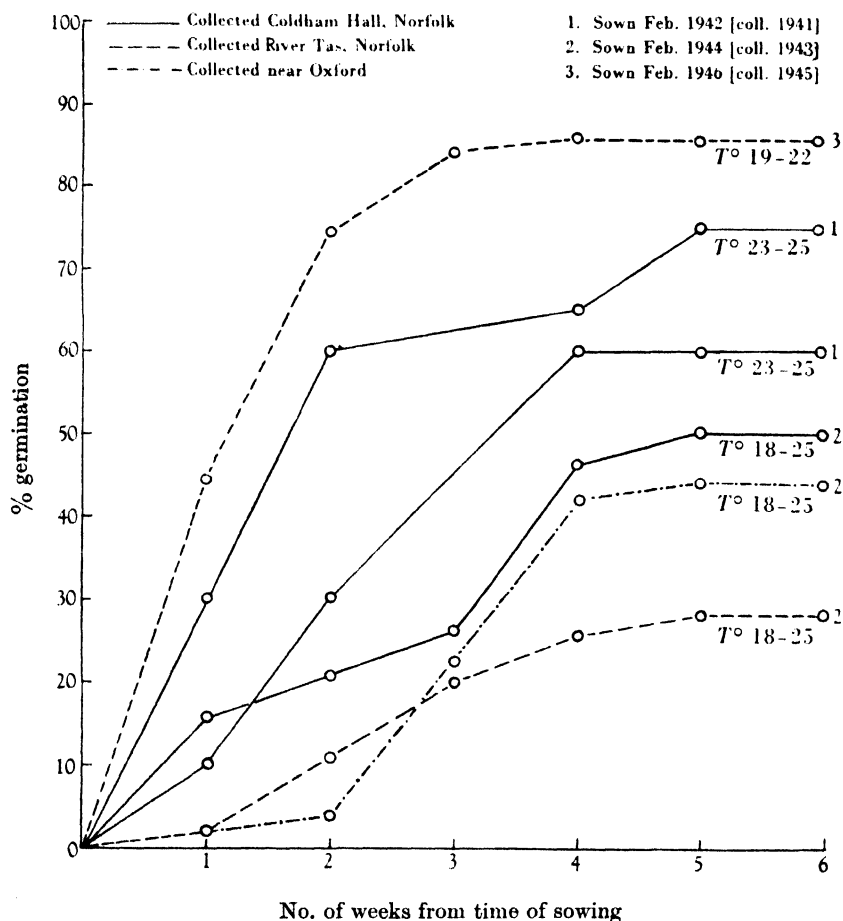


Fig. 4. Graphs showing progressive germination of *Glyceria maxima* grains, after six months' dry storage in laboratory.

(c) *Cleistogamy*. Not reported.

(d) *Apomixis*. No information.

(e) *Vivipary*. Masters (1869, pp. 168-9), referring to vivipary in grasses, includes *Glyceria aquatica* (*maxima*) and *G. fluitans* amongst species 'most commonly affected in this manner'. However, macroscopic examination of representative fresh and herbarium material shows that the 'viviparous' appearance is given by elongation of the ovary accompanied in more advanced cases by proliferation of the floret axis to produce a small leafy shoot emerging from the ovary apex; small roots may be produced from the base of

the proliferating floret, which is easily detached at this stage. Within affected florets, stamens remain present but may be reduced, lodicules become enlarged and membranous, paleas are occasionally reduced, while lemmas remain normal. Small erect club-shaped emergences, at present of unknown significance, are frequently found arising from the base of the proliferation, internal to the stamen whorl.



Fig. 5. False 'vivipary' in florets of *Glyceria maxima*. A, ovary enlarged with reduced stigmas, stamens normally developed; B, as for A, but patches of brand-spores borne on ovary; C, more advanced stage, with first leaf and adventitious roots emerging, stamens reduced and withered, palea somewhat reduced; C', dissection of base of C, to show enlarged membranous lodicules and origin of roots.

Macroscopic evidence so far at hand suggests that this false 'vivipary' may be resultant upon late infection of the flowering axis by *Ustilago longissima* (§ IX (d)). Though connexion with *Ustilago* infection not always traced, in several cases subtending peduncles of 'viviparous' heads were found to carry numerous patches of brand-spores; in others, brand-spore sori were found on enlarged ovary itself; while again, similar patches were found on emerging leaves of the proliferating axis. It is probable that the 'viviparous' forms referred to by many British and Continental writers have a similar origin.

(f) *Hybrids*. No known records. C. E. Hubbard states that the specimen referred to in *B.E.C. Report* for 1931, p. 678, as a possible hybrid with one of the forms of *Glyceria fluitans* actually shows no evidence of hybrid origin.

Table 7. *Number of Glyceria maxima caryopses produced per panicle*

Date of collection	Locality	No. of panicle	Rel. size panicle	Total no. florets in panicle	Total no. mature caryopses in panicle	% fertile florets
27. viii. 43	Marsh by R. Tas, Norfolk	1	Fairly large	3130	198	6.3
"	" "	2	Medium	2667	100	3.7
"	" "	3-12 (10 heads together)	All medium	Not counted	133 (av. for 10)	—
25. viii. 43	Secondary fen at Coldham Hall	13	Medium	2423	221	9.1
"	" "	14	Small	Not counted	63	—
"	" "	15	Medium	"	308	—
"	" "	16-25 (10 heads together)	All medium	"	154 (av. for 10)	—
16. ix. 43	By side of Home Dyke, Wheatfen	26	Large	"	762	—
"	" "	27	Medium to large	"	781	—
"	" "	28	Medium	"	428	—
"	" "	29	Small	"	227	—
"	" "	30	Medium	2780	498	17.8
"	" "	31	"	2360	347	14.7
21. viii. 45	Marsh by R. Tas, Norfolk	32-37 (6 heads together)	All medium	Not counted	305 (av. for 6)	—

(g) *Amount of seed*. Great discrepancy exists in literature consulted, due mainly to confusion as to whether term 'seed' refers to hulled grain, or complete detached floret (which may or may not contain a grain); general impression gathered that seed production is low throughout its geographical range.

Observations on material collected in Oxfordshire and Norfolk since 1939 indicate that seed production has been very small in relation to total number of florets per panicle. Although plants give external appearance of seeding heavily, most of lemmas are empty, and more than half the spikelets produce no seed at all; in others, a well-formed caryopsis occurs only in basal floret, and occasionally also in one above; the next floret in the series may produce a small withered caryopsis. Very rarely, a mature caryopsis is produced by terminal floret, the lower florets of the spikelet being sterile. Table 7 is thought to be fairly representative of number of mature caryopses produced per panicle: though actual counts were only made in 1943 and 1945, general observation showed no great variation in seed production in the other years since 1939.

Table 7 shows higher proportion of mature caryopses produced in panicles from Home Dyke, Wheatfen (panicles 26–31) than from other habitats; this was correlated with later flowering than the rest, and with an appreciably smaller grain than is usual for the species (average size for forty of these naked grains was 1.51 by 0.83 mm. (range 1.28–1.68 by 0.73–0.90 mm.) compared with average of 1.71 by 0.95 mm. (range 1.51–1.90 by 0.80–1.08 mm.) for grains collected from six other habitats in Norfolk and Oxfordshire).

Average-sized caryopses collected from Broads Marsh, Wheatfen, in August 1941, and weighed in November of same year, gave an average weight of 0.0796 g. for 100 grains (four sets weighed, range 0.0785–0.0814 g.).

(h) *Dispersal*. Spikelets carrying well-developed caryopses in basal florets are generally detached entire above the non-flowering glumes as soon as caryopses are ripe; fertile florets subsequently easily separated from sterile florets above them. Majority of the completely sterile spikelets remain attached to the panicle until it dies down at end of the year.

In marginal and reedswamp *Glycerieta*, dispersal of grains probably takes place mainly by water transport. Naked caryopsis is heavier than water, but when shed is completely enclosed by persistent lemma and palea which give buoyancy to grain by entrapping air (cf. Ridley, *Disp. pls.* pp. 193, 240). In still water, both naked and enclosed grains may be held almost indefinitely at surface by surface tension; in disturbed water, naked caryopses sink almost immediately, while enclosed grains may remain at surface for several hours; after about 30 min. immersion, however, they remain floating (in a vertical position) only by virtue of a small air bubble held between tips of enclosing palea and lemma.

In tests made December 1945, using twenty enclosed grains (collected previous August) placed in a jar half-full of distilled water and shaken gently and intermittently, minimum time of flotation of individual grains was 50 min., and maximum 21 hr. 50 min.; majority of grains sank within 12 hr. Praeger (1913), using dry grains (presumably unhulled) shaken up vigorously in a test-tube of water with subsequent shakings at twice-daily intervals, gives a flotation-period of 5 days.

In marsh and fen *Glycerieta*, enclosed cast grains on the ground are probably already waterlogged by time of winter flooding, and hence of doubtful buoyancy. In soft muddy habitats, transport of grains on feet of wading birds, etc., is probably frequent.

(i) *Viability*. Audas (1925, p. 366, introduced Australian material) reports that seed soon becomes infertile, but that fertile seed falling from plant direct to ground will germinate quickly (but cf. § VII (e)).

Grains stored dry in large corked tubes under laboratory conditions are perceptibly withered after 3 years. Decrease in viability of grains of some samples after 2½ years' dry storage is indicated in Table 8.

(j) *Conditions affecting germination*. No significant differences were recorded from two separate experiments in which comparable sets of grains were germinated in laboratory in daylight and darkness.

Grains stored at laboratory temperatures give up to 90% germination in following spring without interim freezing. No significant difference in percentage germination after 5 weeks was recorded from an experiment in which one batch of grains was cooled by burying in snow for 2 days immediately before sowing (February), while other batch remained throughout at laboratory temperature.

Results of preliminary experiment with two natural soils of widely differing pH (grains

sown February at laboratory temperature) showed both initial germination and subsequent development to be definitely inhibited in more acid soil (see Table 9).

Results of subsequent experiments, one with natural soils, the other using range of buffer solutions (Clark, 1928), are shown graphically in Fig. 6. Allowing for difference in time of year of sowing, results indicate significant inhibition of initial germination, together with subsequent arrest in development of a number of seedlings, at the lower pH values (below pH of about 4 in natural soils, pH of 5 in buffer solutions).

(k) *Morphology of seedling.* Development of seedling takes place rather slowly (cf. Stebler (1898), p. 96, Switzerland); time intervals given below for various stages represent minimum for February sowing in laboratory at temperature of 18–22° C.

Table 8. *Percentage germination of Glyceria maxima grains after storage under laboratory conditions*

Germination tests made on samples of fifty grains each, except in case of 1941 grains (twenty grains). Sown in Petri dishes on damp filter paper at approx. temp. range of 18–25° C. Percentages based on no. grains germinated at end of 5 weeks from sowing (cf. p. 329).

Date sown	Time stored	Dates collected							
		1941	1942	1943				1944	1945
		Coldham Hall	Coldham Hall	Coldham Hall	Ranworth Marsh	Blenheim Marsh	Kennington Lane R. Tas		R. Tas
11. ii. 42	5 m.	75	—	—	—	—	—	—	—
12. ii. 44	1 y. 5 m.	2	—	—	—	—	—	No grains collected this year	—
	5 m.	—	80	50	18	44	40	28	—
19. ii. 46	4 y. 5 m.	0	—	—	—	—	—	—	—
	3 y. 5 m.	—	6	—	—	—	—	—	—
	2 y. 5 m.	—	—	52	10	No test	12	76	—
	1 y. 5 m.	—	—	—	—	—	—	—	—
	5 m.	—	—	—	—	—	—	—	84

Table 9. *Germination of Glyceria maxima grains in natural soils of differing pH*

Type of soil used	Initial pH of soil (electrometric)	% germination after 5 weeks	
		Well-developed seedlings	Seedlings with development arrested after emergence of radicle
Silt from <i>Glyceria</i> marsh	7.6	40	—
Acid moor peat	3.6	4	6

Caryopsis coat generally begins to split in region of embryo 3–4 days after sowing; embryo bulges laterally through split, and shows well-defined epiblast (Fig. 7 A). At first, elongation of coleorhiza is slightly in advance of that of coleoptile; coleorhiza and epiblast both enlarge greatly, and both develop long unicellular hairs at about the sixth day (Fig. 7 B, B'). Slender empty tip of coleorhiza turns upwards, and primary root (when sufficiently developed) emerges laterally near proximal end of coleorhiza (Fig. 7 C); primary root does not persist long, and in many cases does not emerge at all (Fig. 7 E). First leaf breaks through coleoptile tip after about 14 days; at same time, two adventitious roots emerge laterally on either side of the plumule, followed shortly afterwards by appearance of third root which generally (always?) emerges from side of plumule away from grain. In etiolated seedlings, where mesocotyl is well-developed, first-formed adventitious roots



are seen to arise from distal end of mesocotyl itself, with their vascular supply leaving the mesocotylar strand below the point where the latter branches to supply the coleoptile and young leaves; exceptionally, one or more additional roots are developed at proximal end of mesocotyl (Fig. 7 H). Subsequent root-development takes place rapidly from basal nodes of young shoot. In laboratory-germinated seedlings, sown late February and planted outside at end of April, first tillers appeared above ground by third week in May, and

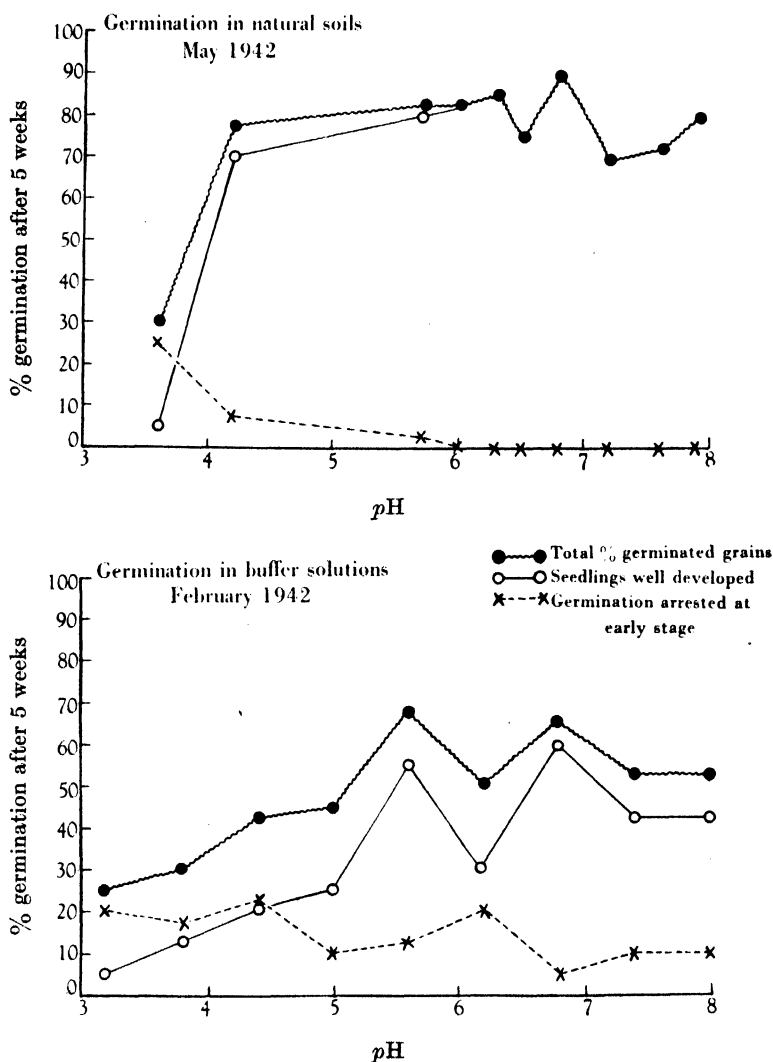


Fig. 6. Germination of *Glyceria maxima* grains at varying pH.

by end of June maximum number of tillers produced by any one plant was 4 (average 2.7 for ten plants).

In experiments with grains sown on sterile soil in flasks under 20, 30 and 40 cm. of water, great majority of seedlings found to float to surface just after emergence of first leaf from coleoptile; if primary root is insufficiently developed to provide anchorage at early stage, the adventitious roots are generally developed too late to counteract increased buoyancy of seedling at later stage. Such flotation may well be effective in dispersal of seedlings to new habitats.

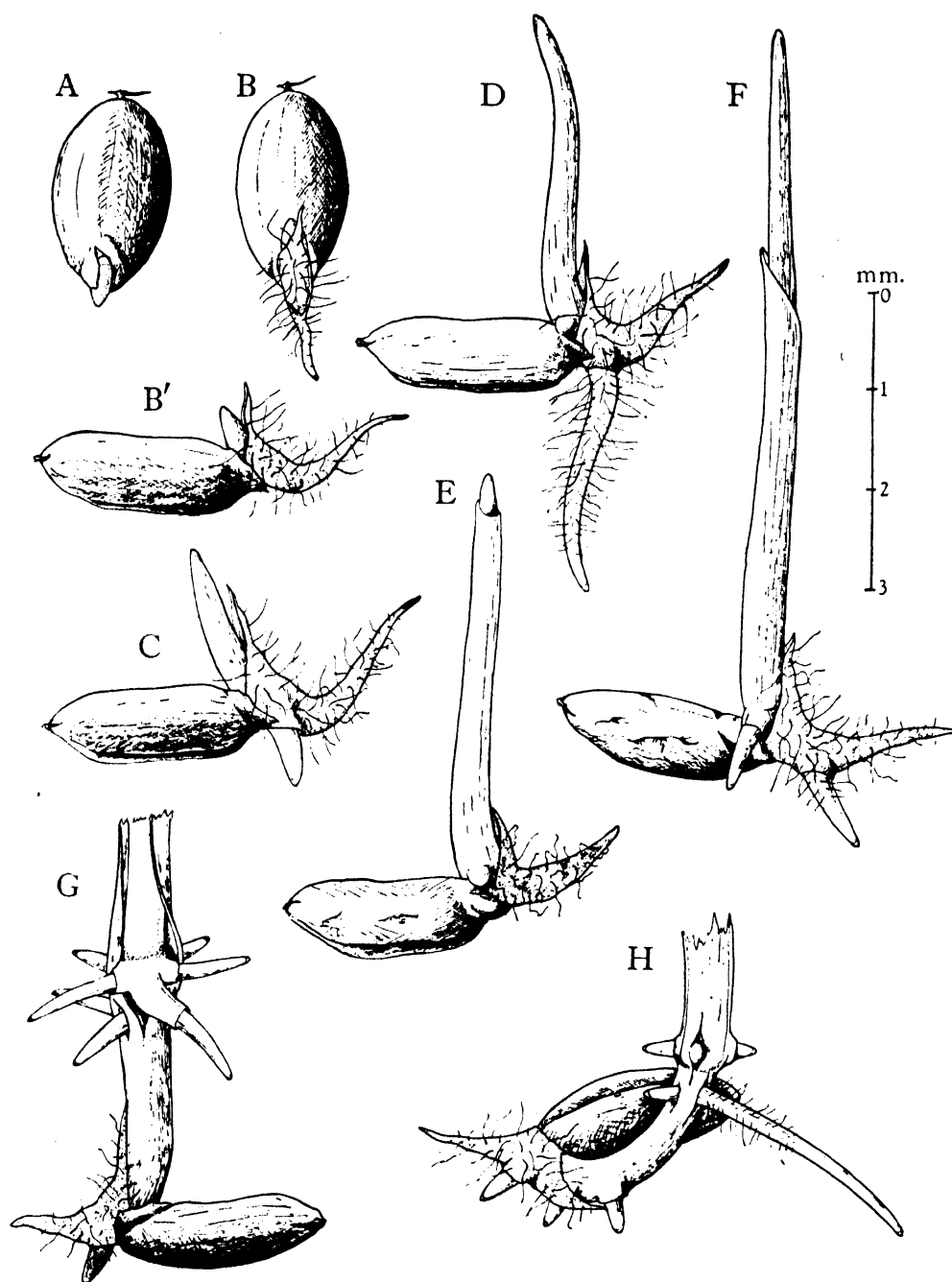


Fig. 7. Early stages in germination of *Glyceria maxima* grains. A-F, grown in light; G, H, in darkness. All grains sown on damp filter paper under laboratory conditions. A, B and B', C, the same seedling 4, 6 and 9 days respectively after sowing; D, E, two fourteen-day-old seedlings, D, with primary root well developed, E, with no emergence of primary root from coleorhiza; F, 21-day-old seedling showing development of one of first two lateral adventitious roots; G, H, 22-day-old etiolated seedlings with elongated mesocotyl, showing origin of adventitious roots in relation to latter.

(l) *Effective reproduction.* Reproduction in dense stands of *Glyceria* seems to be entirely by vegetative means; no germination of grains yet observed in such stands. The only well-established seedlings yet found in natural habitats are those which colonized wet bare mud at Blenheim exposed by lowering of water-level of lake during drought (cf. p. 326); it is possible, however, that colonization of isolated ponds and ditches may be initiated by grains transported on feet of wading birds, etc. (cf. Walker, 1946).

IX. *Parasites, diseases, etc.* (a) *Insects associated with Glyceria maxima* (O. W. Richards). Although a number of insects are recorded as attacking '*Glyceria*' (species not further identified), it seems from the literature that *G. maxima* has to a considerable extent a peculiar fauna. In the following list, therefore, only insects more or less closely attached to that species are recorded.

## HEMIPTERA—HOMOPTERA

APHIDIDAE: *Sipha glyceriae* (Kalt.) (*schoutedoni* Del. Guerc.), widespread in Britain on *Glyceria* (including *G. maxima*) and other grasses.

## THYSANOPTERA

THRIPIDAE: *Baliothrips dispar* (Hal.), common in Britain; also Northern Ireland. Two generations a year on leaves of grasses (including *Glyceria maxima*), producing small, bleached patches. *Euchaetothrips kröli* (Schille), apparently common at least in south, especially on *Glyceria maxima*; habits like preceding, but producing larger patches (G. D. Morison).

## COLEOPTERA

CHRYSOMELIDAE: *Donacia semicuprea* Panz., local but widespread in Britain, adult on leaves, larvae on roots; less commonly on *Sparganium* (cf. Varley, 1939).

## DIPTERA

CECIDOMYIIDAE: *Octodiplosis glyceriae* (Rübsaamen), reddish larvae in leaf-bases, Durham (Bagnall & Harrison, 1922).

AGROMYIDAE: *Agromyza nigripes* Mg., larva mines leaves of various grasses (including *Glyceria maxima*).

## HYMENOPTERA

TENTHREDINIDAE: *Selandria sixii* Voll., larva on grasses, *Scirpus* and *Juncus*; seen to oviposit on *Glyceria maxima* in Norfolk (E. A. Ellis).

## LEPIDOPTERA

NOCTUIDAE: *Leucania straminea* Treits., larva on *Glyceria maxima* and other Gramineae, southern half of Britain, Ireland.

PYRALIDIDAE: *Schoenobius forficellus* (Thnbg.), larva in stems, England to Yorks, Ireland.

ELACHISTIDAE: *Elachista poae* Staint., larva mines leaves, southern England.

In preparing the above lists, valuable assistance was given by Dr H. F. Barnes, Mr R. B. Benson, Mr E. A. Ellis, Mr C. T. Gimingham, Dr A. M. Massee, and Dr G. D. Morison.

(b) *Parasitic and saprophytic fungi associated with Glyceria maxima* (E. A. Ellis). Records based mainly on observations in Norfolk, especially in Yare Valley.

## ASCOMYCETES

**HYPOCREALES:** *Nectriella dacrymycella* (Nyl.) Rehm, develops on soft dead culms which have not quite settled down into the 'mat' in late summer; found also on associated *Typha latifolia*, *Iris pseudacorus* and *Carex* spp. *Gibberella zeae* (Schwein.) Petch, very common on dead culms and leaves of *Glyceria maxima* throughout the year, frequently developing on procumbent shoots killed prematurely by *Ustilago longissima*. No *Fusarium* conidia have been found associated with it on this host, but an 'Oospora' bearing resemblance to *O. penicilloides* (Riv.) Sacc. (originally described as occurring on rotting and damp hay respectively, in Italy) precedes the *Gibberella* on dying and very newly dead leaves, chiefly in autumn and winter. *Gibberella zeae* is fairly common on *Phragmites* growing with the *Glyceria* and has been found occasionally on *Carex riparia* (with the *Oospora*) and *Typha latifolia* in the same community. *Tubeufia helicomycetes* v. Höhn. (? *Ophionectria paludosa* (Crouan) Sacc.), superficial on soft rotting culms of the *Glyceria* 'mat', May to August; closely accompanied by *Helicosporium phragmitis* in one locality and *Ciliospora albida* in another.

**SPHAERIALES:** *Chaetomium elatum* Kze. & Schmidt ex Fr., found on *Glyceria maxima* only after it has been stacked as litter. *Anthostomella tomicum* (Lév.) Sacc., occasionally on dead leaves of *Glyceria maxima*, but more commonly on *Cladium*; found also on *Juncus*, *Typha* and marsh grasses. *Rosellinia* sp., superficial on dead culms of *Glyceria maxima* growing with *Carex acutiformis* or *C. riparia* with which the fungus is chiefly associated. *Niesslia exosporioides* (Desm.) Wint., maturing on dead culms in late summer and autumn; most common on *Carex* spp., but sometimes on *Glyceria maxima* and *Iris pseudacorus*. *Sphaerella tassiana* de Not., on rather newly dead culms and leaves in autumn.

**HYSTERIALES:** *AcrospERMUM compressum* Tode ex Fr., maturing on soft dead leaves of *Glyceria maxima*, *Phragmites*, *Carex*, *Iris* and *Typha latifolia*, April to July in marshes, and on herb stems in other habitats in late winter and spring.

**PHACIDIALES:** *Lophodermium arundinaceum* (Schrud. ex Fr.) Chev., common on *Glyceria maxima* and other marsh grasses; maturing in spring.

## BASIDIOMYCETES

**TREMELLALES:** *Tremella uliginosa* Karst., abundant on decaying leaves of *Glyceria maxima* under willows in autumn (Wheatfen Broad and Bradeston, Norfolk).

**USTILAGINALES:** *Ustilago longissima* (Sow. ex Schlecht) Meyen, a serious disease (see later part of this section—IX (d)).

**AGARICALES:** *Peniophora longispora* (Pat.) v. Höhn. & Litsch, rather common on haulms of *Glyceria maxima* and other marsh grasses. *Epithele typhae* (Pers. ex Fckl.) Pat., occasionally spreading over dying leaves of *Glyceria maxima*, September to November; occurring most commonly on leaf-bases of *Carex* spp., and occasionally on *Typha*. *Pterula multifida* Fr., common on soft, newly dead leaves of *Glyceria maxima*, late summer and autumn. *Omphalia gibba* Pat., occasionally on soft dead culms of *Glyceria maxima* as well as on *Cladium*, *Carex* and *Phragmites*. *Mycena quisquiliaris* (Gosselin) Kuehn., occasional on dead leaves of *Glyceria maxima* in autumn, also on *Cladium*. *Coprinus urticaecola* (Berk. & Br.) Buller or *C. friesii* Quel., common on bases of living stems and on fallen culms and leaves of *Glyceria maxima*, where it is frequently submerged in water; a similar, probably identical, fungus occurs in similar situations on other associated reedswamp species.

## FUNGI IMPERFECTI

SPHAEROPSIDALES: *Phoma* aff. *lineata* Sacc., on dry dead culms; spring. *Ascochyta graminicola* Sacc., on fading leaves of various grasses, including *Glyceria maxima*; summer and autumn. *Ciliospora albida* (Mass. & Crossl.) Grove, found in abundance on stems and leaves of *Glyceria maxima* trampled by cattle throughout several acres of marshes at Old Lakenham, Norfolk, July to September 1942; apart from this instance, has been found only rarely and in small quantities on *Epilobium*, *Caltha* and *Equisetum*. *Microdiscula phragmitidis* (West.) v. Höhn., occasional on *Glyceria maxima*; common on dying culms of *Phragmites* and *Phalaris*.

MELANCONIALES: *Cryptomela typhae* (Peck) Died., normally on *Typha latifolia* and *T. angustifolia*; found once on leaf-bases of *Glyceria maxima* at Wheatfen Broad, Norfolk, 18 Sept. 1943.

MONILIALES: *Trichoderma viride* Pers. ex Fr., patches on newly dead leaves on surface of 'mat' in autumn. *Torula herbarum* Link ex Fr., occasionally on dead culms above leaf mat in spring, similarly on *Carex*; most common as saprophyte on dead herb stems. *Papularia sphaerosperma* (Pers. ex Fr.) v. Höhn., very common on *Phragmites*; twice found on stems and leaves of *Glyceria maxima* after these had been scorched by marsh fires. *Dematium hispidulum* Fr., appears on newly dead leaves in autumn and persists until following summer; *Glyceria maxima* appears to be more commonly frequented by this fungus than any other grass in Britain. *Cladosporium herbarum* Link ex Fr., common and ubiquitous on dying marsh vegetation in autumn; appearing on dying infructescences of *Glyceria maxima* for short time. *Helicosporium phragmitis* v. Höhn., a characteristic fungus of decaying stems of *Glyceria maxima* in basal leaf mat, found regularly on the *Glyceria* in Yare Valley, and occasionally on *Phragmites*, *Phalaris arundinacea* and *Calamagrostis canescens*. *Sporocybe rhopaloides* Sacc. & Roum., occasionally on newly dead leaves of *Glyceria maxima* and associates; mainly on *Carex*; most flourishing April to July. Shoots killed prematurely by stem-boring insects are often attacked soon afterwards by *Sporocybe*. *Volutella arundinis* (Desm. ex Fr.) Sacc., common on newly dead leaves of *Glyceria maxima* and associates in autumn and winter. *Volutella melaloma* Berk. & Br., maturing on overwintered dead leaves of *Glyceria maxima*, *Carex* and *Typha*, chiefly in spring. *Epicoccum diversisporum* Preuss, on newly dead culms, often associated with *Cladosporium herbarum* in autumn.

(c) *Mycetozoa* associated with *Glyceria maxima* beds in Yare Valley, Norfolk (E. A. Ellis and H. J. Howard).

*Physarum psittacinum* Ditmar, **P. nutans** Pers., *P. cinereum* Pers., **P. sinuosum** (Bull.) Weinm., *P. contextum* Pers., **Craterium minutum** (Leers) Fr., **C. leucocephalum** Ditmar, *Leocarpus fragilis* (Dicks.) Rost., *Diderma radiatum* (L.) Rost., *Diachaea subsessilis* Peck., *Didymium difforme* (Pers.) Duby, **D. clavus** (Alb. & Schw.) Rost., **D. squamulosum** (Alb. & Schw.) Fr., **Mucilago spongiosa** (Leysser) Morgan, **Comatricha tenerima** Lister, *Lamproderma scintillans* (Berk. & Br.) Morgan, *Trichia varia* Pers., **Arcyria cinerea** (Bull.) Pers., *A. pomiformis* (Leers) Rost.

Those species printed in heavy type may be considered as common in this community.

(d) *Serious diseases*. The smut, *Ustilago longissima* (Sow. ex Schlecht.) Meyen attacks the living leaves of *Glyceria maxima* almost everywhere, and occurs less commonly on *G. fluitans* and *G. plicata*. Longitudinal spore-filled channels, soon opening to the exterior, are formed between the vascular bundles of the leaves. According to Plowright (1889),

attack by *Ustilago* prevents flowering; the effect of the smut on the development of the inflorescence in a potentially flowering shoot is, however, dependent upon time, place, and intensity of infection. Shoots heavily infected early in the growing season elongate rapidly, forming slender stems bearing rather crowded, small, yellowish leaves with longitudinal lines of spores; affected shoots die back much earlier than healthy ones. A few scattered sori appear sometimes on leaves of flowering shoots late in the season; late infection of the inflorescence is thought possibly to have some connexion with the falsely 'viviparous' appearance of some heads (§ VIII (e)).

Some confusion exists in literature as to possible deleterious effect on cattle of plants affected with *Ustilago* (cf. Eriksson, 1912, p. 60, 1930, p. 138; Strecker, 1923, p. 510; Mentz, 1935, p. 64; Petersen, 1936, p. 143). Some serious cases of stock-poisoning from this cause reported by Eriksson (1912, 1930), while certain German names (Platzgras, Berstegras) given to the affected grass originate from a recognition of its poisonous qualities (Aschers. & Graebn. 2); it seems agreed, however, that any such poisonous properties are confined to the fresh grass, and that dried hay seems harmless.

X. *History*. No information as to fossil record.

As 'leyt', was referred to in Manor Rolls of Littleport of early fourteenth century (earliest non-botanical British reference traced); described in Gerard's *Herbal* (1597, p. 6) as 'Gramen majus aquaticum . . . in fennie and watery places . . .' (first botanical reference).

XI. *Economic uses*. Was earlier considered a valuable fodder crop in Britain, especially in East Anglia where extensive natural stands occurred; here, was once the principal grass of the Wash lands (i.e. the lateral waste areas embanked 'for the rivers to bed in' at time of flood), and composed the bulk of the 'fodder' obtained from such localities (Miller & Skertchley, 1878, p. 297). Deemed worthy of special mention by Camden (1586) in his 'Britannia', who states of the Fenland 'it so strangely abounds with a rich grass and rank hey (by them call'd *lid*) that when they've mown enough for their own use, in November they burn up the rest, to make it come again the thicker' (trans. Gibson, 1695, p. 407). Curtis (1777) quotes it as one of the most useful of British grasses, constituting 'a great part of the riches of Cambridgeshire, Lincolnshire and other counties where draining land by means of windmills has taken place. . . [It] not only affords rich pasturage for their cattle in the summer, but forms the chief part of their winter fodder.' According to Sinclair (1816), 'the inhabitants [of the Isle of Ely] call it fodder by way of eminence, other kinds of coarse hay being called stover, i.e. "coarse stuff"'; he notes also that it afforded abundant hay crops along the Thames.

Harvesting of *Glyceria* crops in Britain recently very greatly restricted owing to increasing labour costs; in region of Yare Broad (where local report states that in last century *Glyceria* hay was sent as far as London for fodder for cab-horses), the *Glycerieta* are now only cut regularly on one estate; cutting on the other marshes ceased some 20-30 years earlier, except for local requirements.

On Continent, value as forage plant recognized in some European countries by eighteenth century, but not extensively grown (Clark & Malte, 1913, p. 71); planted, however, fairly extensively in Scandinavia, mainly during nineteenth century (Holmberg, 1926, p. 229). In Germany, natural stands of *Glyceria* were prized for their fodder value to very recent times (cf. Petersen, 1936, p. 220; Klapp, 1937, p. 153); Weber (1928) states that it is particularly valued as feed for dairy cows, and is reputed to have similar effect on milk production as green maize. In searching for natural resources of forage plants in Russia,

Košurnikova & Stróková (1939, pp. 220–1) suggest that natural stands of the grass may give a considerable weight of nutritious fodder and prove useful for silage; computed yield of up to 170 centners per hectare of dry weight given for individual stands (cf. Petersen (1936): 'possible to obtain up to 150 dz. (300 centners) hay per hectare from *Glyceria* meadows of good type').

Rootstocks for planting out have been distributed on a commercial scale in Australia during last 20 years (cf. § I (b)); here of value mainly for reclaiming swamps and providing summer fodder for dairy cows.

General agreement in literature that it should be cut before panicle emergence for full fodder value, though owing to late lignification, can be used for hay up to time of flowering (Klapp, 1937); aftergrowth generally used for litter. Scandinavian material showed coefficient of digestibility at time of panicle emergence almost equal to that of ley grass and considerably exceeding that for reed hay (Axelsson & Hellberg, 1942). Sugar and protein content high (cf. Table 10).

Table 10. *Analysis of chemical composition of Glyceria maxima crops*

(1) *Scandinavian material, harvested at beginning of panicle emergence* (Axelsson & Hellberg, 1942).

	Percentage composition of dry matter				
	Crude protein	Crude fat	N-free extractives	Fibre	Ash
Green fodder	11.2	3.3	42.5	30.7	12.3
Hay	11.5	2.6	43.5	30.4	12.0

(2) *Material from Neerim, Gippsland, Australia; harvested in flower.* Analysis by W. R. Scott, Agric. Chemist of Dept. of Agriculture, Victoria—incorporated in commercial pamphlet by Law, Somner Pty. Ltd. (date not known).

Percentage analysis on dry basis				
Protein	Fat	Carbohydrates	Fibre	Ash
7.67	1.94	54.72	29.07	6.60

Fresh material of *Glyceria* is reported to contain a high proportion of hydrocyanic acid (cf. Guérin, 1932, pp. 1036–7; Minssen, 1933); Minssen regards it as richest of all French indigenous plants in this compound. The acid is present in all organs of the plant except the fruit, the highest proportion occurring in young leaves; there is a noticeable diminution in cyanogenetic glucoside as leaves mature, and at later stage, highest proportion is found in inflorescences (Guérin, 1932). Minssen gives value of 25–80 mg. hydrocyanic acid per 100 g. dry matter for young grass, with much smaller proportion in older straw-like grass or hay. Hydrocyanic acid content remains constant for several years in good air-dry hay. Quantity of hydrocyanic acid present, however, rarely seems deleterious to stock.

Among minor uses of *Glyceria* may be included its occasional employment for thatching, both in Britain (Pratt, 1873) and abroad (Aschers. & Graebn. 2); has also been used by country people as packing material for goods (Pratt, 1873), and in Norfolk as binding material in construction of building blocks. In sporting estates, is esteemed highly as covert for water fowl (cf. Johns, 1919).

Despite its economic value, however, may quickly become a pest unless effectively controlled, owing to its very rapid overgrowth of drainage dykes and choking of slow-flowing rivers. In New Zealand, though only introduced comparatively recently (p. 315), has already become a sufficient nuisance in certain parts for rigid control to be advocated (Walker, 1946).

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*ATROPA* L.

One British species

*Atropa belladonna* L.

R. W. BUTCHER

A large, erect, herbaceous perennial, 50–200 cm. high, with long tapering branched roots, 0.5–7 cm. diam.; stem erect, solid, terete, either glabrous or densely covered with fine, short hairs; first branch (the crutch) about 25 cm. from the base; leaves broadly ovate, often asymmetric, acuminate, smooth, green, entire, single and alternate on the lower stem, borne in unequal pairs on the portion above the crutch.

Flowers pentamerous, axillary, solitary in each leaf-axil, drooping; calyx conspicuous, green, dilated in fruit; corolla campanulate, purple; the stamens included, but with very obvious yellow anthers; fruit a smooth, purple or almost black, 2-celled berry about 2 cm. diameter.

No British varieties have been described and the most marked forms are due to varying quantities of anthocyanin and to the density of the hairs, so that green-stemmed or purple-stemmed, nearly yellow or deep purple flowered, or densely and slightly hairy forms may be found. The shape of leaf, calyx and corolla also vary. Many of these forms are being studied by R. Melville and W. O. James.

In Britain it occurs locally as an apparent native in open vegetation on calcareous soil, also spontaneously and as a relic of former cultivation as a medicinal herb.

I. *Geographical and altitudinal distribution.* The distribution in Britain as a native plant is correlated with the principal chalk and limestone formations as follows:

(a) *The chalk scarp of the South Downs.* The most easterly recorded place is Black Cap east of Lewes, it is abundant around Arundel, Marden Forest and Goodwood in Sussex, less frequent in Hampshire with considerable patches near Winchester, Stockbridge and Salisbury, while the most southerly place is Charborough Park near Blandford, Dorset.

(b) *The chalk scarp of the North Downs.* Localities are plentiful from near Canterbury and Wye westwards; to Wrotham in Kent; Dorking, Reigate and Guilford in Surrey, and Whitchurch and Andover in Hants are other places where it can be found, thus making a more or less continuous belt for the whole of the scarp.

(c) *The chalk scarp from Yorkshire to Wiltshire.* The plant is abundant around South Cave, east Yorks, and there are patches near Louth and Bourne (Lincs) and Wisbech (Cambs), but it is rare in these eastern counties, probably because the chalk is largely covered by glacial drift. There is an isolated locality at Horsey on the Norfolk coast (see later) and a few others in Norfolk and Suffolk, chiefly in ruins, while southwards it is found at Newton south of Cambridge and plentifully on the Chiltern Hills from Tring to Streetly (Berks). There are probably other patches in north Wiltshire, but these have not been explored.

(d) *The Oolite Limestone Series.* Although there are one or two records from the Lincolnshire oolite, the plant first becomes abundant farther south in Rutland. There are

patches near Oundle and Northampton (Northants) and Woodstock (Oxon); it then again becomes abundant in the Cotswold Hills. There are isolated patches in Somerset and near Bath. On the Jurassic Limestone of Yorkshire there are several localities in the Cleveland Hills.

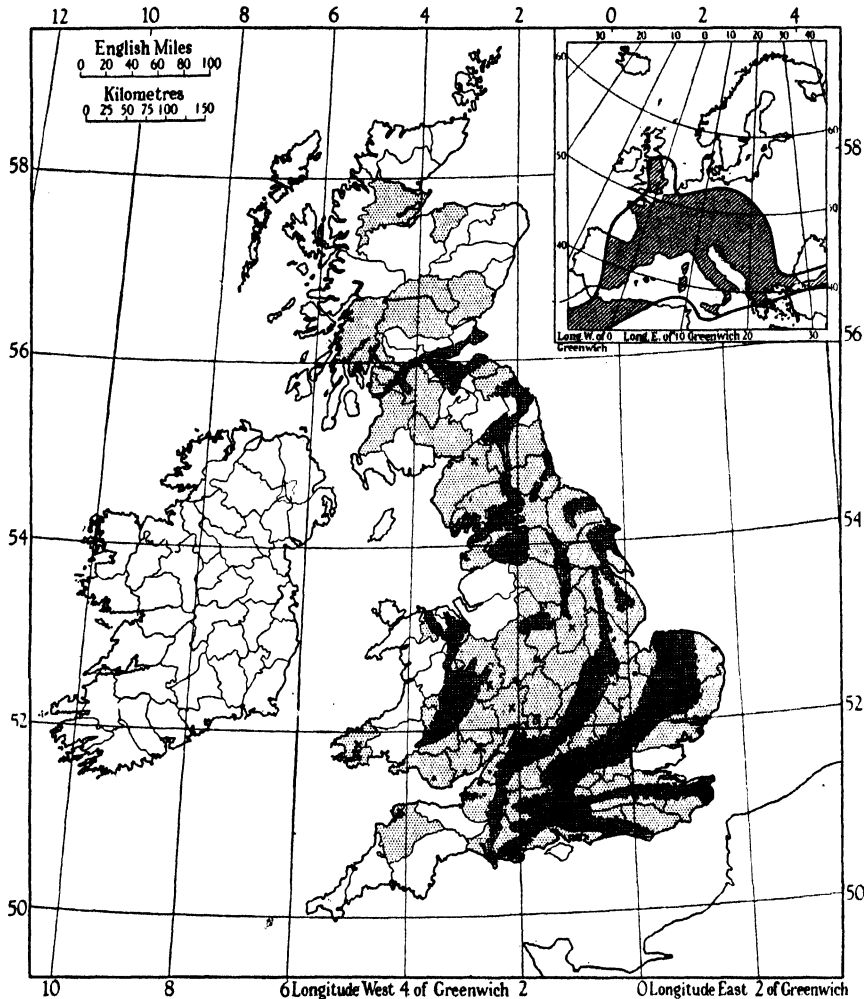


Fig. 1. *Atropa belladonna*. Vice-comital distribution in the British Isles and (inset) approximate distribution in Europe.

- Principal calcareous rocks (close hatching).
- ▨ Vice-comital records (where there is no × the locality has not been ascertained).
- = Authenticated native localities.
- × = Doubtful, casual and introduced localities.

(e) *The Magnesian Limestone*. On this formation the plant is found in several places (though rarely abundantly) in Durham, south Yorkshire, and, as an outlier, near Dudley (Staffs and Worcs).

(f) *The Carboniferous Limestone*. Records here are sparse and uncertain, and it is reasonable to suggest that the plant is not native on most of this formation. It is, however, plentiful in north-west Lancashire and south Westmorland, where there are at least six authenticated records. There is in most cases a single record for each county, often

associated with ruins, suggesting that the plant is not native. Other records, in all of which the plant is rare, are from Devon, Pembroke, Glamorgan, Brecon, Monmouth, Hereford, Montgomery, Shropshire, Flint, Denbigh, Northumberland, Cumberland.

In Ireland it grows on Coney Island in the Shannon estuary, in Counties Donegal and Meath, and is looked upon as a denizen (Praeger, *Ir. Top. Bot.*).

The same remark applies to the Scottish records indicated on the map.

The above include all the apparently native places, but in considering its distribution two human factors must be taken into account. The plant is poisonous, and many deaths have been recorded through children eating the black juicy and pleasantly tasting berries, so every effort is made to exterminate the plant in accessible places. The alkaloids in the plant are used as a drug, and both leaf and root are collected for this purpose, while for the same reason the plant must have been cultivated in some of the odd localities, such as the ruins of castles and monasteries and there it is now a survival.

In some localities it appears from time to time as a weed in gardens and on waste ground, e.g. in Cambridge. In England it is a lowland plant, occurring from sea-level to 220 m. in the Hambleton Hills (Baker, 1899).

In Europe it occurs as an apparently native plant, especially in felled woodlands and mainly in rocky, hilly districts, from Belgium, France, central and eastern Spain eastwards to south-west Poland, Transylvania and Thessaly, extending to Asia Minor, the Caucasus and Persia; north to Cologne, the Ruhr and Volme valleys, Hanover, Mecklenburg, Brandenburg and Silesia in Germany, south to the coast of the western Mediterranean and Dalmatia, reappearing in north Africa in Algeria, the Rif and the Middle Atlas (Jahandiez & Maire, 1931-4). Outside its area as an apparently native plant it is widely distributed as a naturalized plant or escape from cultivation, e.g. in Portugal, Schleswig-Holstein, East and West Prussia, Denmark and Sweden. Ascends to 1650 m. in the Bavarian Alps (Hegi, *Fl.* 5, p. 2567), to 5500 (Italian) ft. (c. 1700 m.) on Monte Baldo in north Italy (Parlatore, 1884-6) and to 2100 m. in the Middle Atlas of Morocco (Jahandiez & Maire, 1931-4).

II. *Habitat.* The plant apparently requires a well-drained calcareous soil, a damp atmosphere and some shade. It attains its greatest development on the steep slopes of stony calcareous woodlands, in old quarry workings and among ruins. Excessive shade usually reduces its vigour though plants have been seen flowering well under yew trees. In quarries there is little natural shade though the steep slopes may reduce the duration of sunlight and no constant orientation to the compass can be found.

As so many of its habitats are on steep slopes, even on cliffs and walls, an open, friable soil seems to be a determining factor. It is exceptional to find the plant among grass or in a closed community, while in the districts where the plant is common it frequently turns up as a garden weed.

Like many plants of the same tribe it is highly nitrophilous and in cultivation responds well to dressings of nitrogen fertilizers (W. O. James), though how such are obtained in the stony soil-free quarries and ruins where the plant often grows has not been determined.

A locality worthy of comment is at Horsey, Norfolk. In 1938 the sea broke through the retaining wall and flooded a large area of cultivated land. After the sea had retreated the first plant to appear in 1939 in great abundance on the bare, previously arable soil was *A. belladonna*, which had been noted as very rare previously; in 1943 it was still growing in a strip of woodland and among nettles on the bank of one of the dykes, and

in 1945 there were still plenty of well-established plants here and in its original locality (E. A. Ellis). The soil here is alluvium and glacial drift. The effect of sea water on the soil was to deflocculate the clay, and this would presumably turn a grass-covered clay land into a bare soil somewhat akin to that on which *A. belladonna* usually grows.

On the Continent in meadows and deciduous woodland, preferring, but not, as in Britain, restricted to calcareous soils. In central Europe (Hegi, *Fl.* 5) a characteristic plant of felled woodland, especially in the Montane Region of the central and southern districts. In Graubünden (Switzerland) a plant of felled woodland in the warmer areas, not persisting in the same locality, on humus-rich soil overlying all types of rock, chiefly in the beech region (Braun-Blanquet & Rübel, 1934).

III. *Communities.* *A. belladonna* is sometimes found under the shade of trees accompanied by no other plant. It is almost always in an open community dominated by *Sambucus nigra* and *Urtica dioica*. Other associated plants which are frequently present can be illustrated from the following localities:

(a) Woodland slope, Boston Spa, Yorks. *Sambucus nigra* c.d., *Urtica dioica* c.d., *Arctium lappa* f., *Mercurialis perennis* f., *Bryonia dioica* f., *Rubus caesius* f., *Glechoma hederacea* o., *Verbascum thapsus* o.

(b) Woodland slope, Arnside, Westmorland. *Sambucus nigra* c.d., *Urtica dioica* c.d., *Mercurialis perennis* a., *Glechoma hederacea* f., *Scrophularia nodosa* f.

(c) Woodland slope, West Burton, Sussex. *Sambucus nigra* c.d., *Urtica dioica* c.d., *Ligustrum vulgare* f., *Arctium lappa* f., *Mercurialis perennis* f., *Bryonia dioica* f., *Lithospermum officinale* o.

(d) Quarry debris, Tadcaster, Yorks. *Urtica dioica* d., *Sambucus nigra* f., *Inula conyza* f., *Bryonia dioica* f., *Arctium lappa* f., *Rubus caesius* o., *Verbascum thapsus* o.

(e) On the steep slope and quarry debris, Kirby Moorside, Yorkshire. *Pteridium aquilinum* d., *Urtica dioica* s.d., *Sambucus nigra* s.d.

The occurrence of *A. belladonna* among bracken is exceptional, though it appears to maintain itself vigorously. Its long tap root enables it to grow in a horizon of the soil different from that occupied by the bracken rhizome and for the same reason it may grow on a surface leached soil among calcifuge plants (e.g. *Digitalis purpurea*).

In felled woodland in central Europe it is associated with *Chamaenerion angustifolium*, *Cirsium vulgare*, *Fragaria vesca*, *Galeopsis tetrahit*, *Populus tremula*, *Rubus idaeus*, *Senecio sylvaticus* and *Sorbus aucuparia* (Hegi, *Fl.* 5); in felled woodland in Graubünden also with *Chamaenerion*, *Galeopsis tetrahit* and *Senecio sylvaticus* (Braun-Blanquet & Rübel, 1934). In the Hercynian Province of Germany, where it inhabits high beech forest, it is found with *Asarum europaeum*, *Cephalanthera damasonium* and *C. rubra*, *Cypripedium calceolus*, *Milium effusum*, *Neottia nidus-avis*, *Ranunculus nemorosus*, *Sanicula europaea*, *Veronica montana* and *Vinca minor* (Hegi, *Fl.* 5).

IV. *Response to biotic factors.* Regenerates from the lower nodes if cut down in spring, often flowering and fruiting in the autumn. It regenerates also after being eaten by sheep (Furness Abbey, north Lancs). There is also a marked increase in the quantity of the plant in woodland (e.g. in the Cotswold Hills) after felling or *coppicing*. Alkaloid content of the plant has been studied by Sievers (1914) and W. O. James (1944). The greatest amounts are in the young stem and leaf and in the root. There is very little in the calyx or in the old woody stem after the leaves have fallen while in the fruit and the fruit juices the quantity is medium. Young stem and leaf have the greatest amounts in April and the

percentage falls steadily through the season. Plants severed from the roots and left in water continue to increase in alkaloid content.

The alkaloid content can also be very considerably increased by dressings of artificial nitrogenous manures. Nitrogen-starved plants soon show a yellow green colour; they are tall and thin with very few side shoots and produce an abnormal amount of purple pigment in stem and leaf tips. In extreme cases the leaves roll in at the edges and drop off prematurely (W. O. James).

Cultivated at Nottingham in a sandy loam deficient in lime the plants were 60–80 cm. high, very red stemmed, and produced five shoots from each crown the second year. They flowered well but produced no fruit.

V. (a) *Gregariousness*. At first there is a single stem to each plant, but afterwards there are up to 18 (average 10) large branches from a single crown. In ruins, plants are often solitary and if there is a larger number of individuals these are never contiguous, that is, the plant is always in an open community.

(b) *Performance in various habitats*. Plants in the open are often dark stemmed and average 35–40 cm. in height (R. W. Crosland). In semi-open places the stem is more or less green and the height 80–100 cm.; where there is some shelter it is 120–150 cm. high, while in moderate shade and ideal conditions it can even exceed 200 cm., e.g. at Streetly (Berks). In extreme shade under yew trees at Humphrey Head, Lancs, the plants were 60–80 cm., very green and sparsely flowering. Plants on ruins and in full sun seem often to be more hairy than those in semi-shade.

(c) *Effect of frost, drought, etc.* Liable to be cut down or scorched by frost and keen winds in exposed positions (R. W. Crosland). After a severe late frost on 26 April 1945, 90% of a group of plants near Louth, Lincolnshire were unaffected but two or three had the top 15 cm. severely scorched. These branched later from the base.

VI. (a), (b) *Morphology, etc.* Root a long vertical gradually tapering and branched fleshy tap root which after 12 months may be 5 cm. diam. and 30–50 cm. long. It thickens annually at a decreasing increment. Fibrous roots rare. Stem wholly aerial rising from the crown of the root which may sometimes be above ground. Stolons produced occasionally, 30–100 cm. long with 1–2 rings of adventitious, fibrous roots.

Root thick, long-tapering little branched 10 mm. in diameter at 1 year old, 20–30 mm. at 2 years and up to 50 mm. in old plants, covered with a blackish brown corky layer.

(c) *Mycorrhiza*. No information.

(d) *Perennation*. Hemicryptophyte. The aerial portion dies away in November leaving dead woody main branches.

(e) *Vegetative reproduction*. Stolons are produced on large plants and the rotting away of the original crown of the root may sometimes result in two or more plants growing where one did before, but vegetative reproduction is apparently not important.

(f) *Longevity*. In cultivation a plant is grown for 4 years when it is dug up for the roots. At Oxford the oldest plant in cultivation is 6 years old and looks to be past its best. The oldest wild individual known in the Chilterns died in its eighth year (W. O. James). It persists for very many years in the same locality in spite of attempted destruction (see under).

(g) *Age at first flowering*. Flowers in the second year, but under very favourable conditions may do so in the first year.

(h) *Frequency of seed production.* Produces seed in the second year and sometimes in the first year in favourable localities; very large quantities are produced every subsequent year.

(i) *Ecotypes.* No information.

(j) *Chromosome number*,  $2n=72$  (continental material) (Mert. Cat.).

VII. *Phenology.* (a) Time of maximum growth of roots appears to be September and October, especially at the end of the first year.

(b) The new shoots from the rootstock appear above ground in February with the leaves folded around the stem. They grow rapidly till mid-April when they are 30 cm. long and then branch.

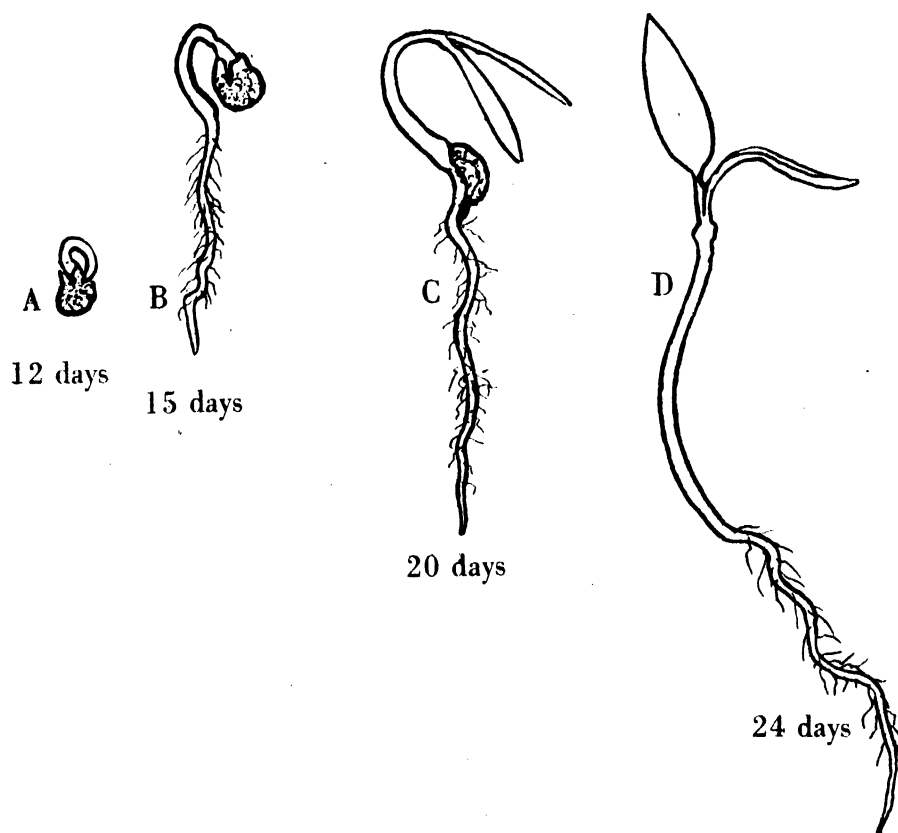


Fig. 2. *Atropa belladonna* L. Stages of germination. A, 12 days; B, 15 days; C, 20 days; D, 24 days. All grown on filter paper, 4 April–1 May 1946.  $\times 10$ .

(c) The first flowers open at the beginning of May. In north Yorkshire they were seen first on 4 May 1944 and 27 April 1945, but it is most unusual to find flowers opening in quantity before the last week of May (R. W. Crosland).

(d) The berries begin to ripen at the end of July. A second flowering period may commence at the beginning of September on plants previously cut down or damaged and some berries may ripen.

(e) A few seedlings are found at times within a few feet of the parent plant on open ground in the spring. They appear to be then 12 months old. Seedlings 2–3 months old have been seen only in the summer months suggesting that germination is only in the early spring.

VIII. (a) *Mode of pollination*. Protogynous humble-bee flower, producing nectar at the base of ovary, and concealed in the lowest contracted part of the corolla (Knuth, *Poll.* 3). When the flower opens the filaments are recurved and the anthers midway down the corolla tube. At this stage the bee touches the stigma first and cross pollination is assured. Within 48 hr. the filaments have equalled the length of the style. The anthers then dehisce and as the flowers are pendulous self-pollination may take place. The base of the corolla tube is closed by hairs at the base of the anthers.

(b) *Insect visitors*. Insects visiting the flowers do not appear to be frequent and have been observed to fly away afterwards as if they did not enjoy their visit (R. W. Crosland, Yorks; Mrs Hutton, Rutland). In Surrey humble bees and honey bees were seen to visit the flowers (R. R. Hutchinson and R. Melville). *Taeniothrips atratus* (Hal.) (Thysanoptera: Thripidae) has been recorded as a visitor (G. D. Morison).

(c) *Cleistogamy*. Not observed and unlikely to occur.

(d) *Apomixis*. Reproduction probably amphimictic.

(e) *Vivipary*. Does not occur.

(f) *Hybrids*. As *Atropa* is a monotypic genus in Britain native hybrids are impossible.

(g) *Amount of seed*. Seeds in a single berry 120; berries on a single main stem 105; stems on a plant 5-12. Only about 3% of the flowers fail to set seed (R. W. Crosland, R. R. Hutchinson). Salisbury (*Rep. Capac.* p. 190) gives the average number of fruits on nine plants as  $473 \pm 73$  and the average number of seeds in twenty fruits as  $155.5 \pm 4.7$ ; the average number of seeds per plant per annum is therefore  $74,045 \pm 13,725$ .

(h) *Dispersal*. Seed dispersal is by birds or by no special method. Berries are still on the plant in December, but afterwards they drop off and gradually disperse in the soil. Birds, especially pheasants, also devour the berries. The seeds adhere to each other and to the ovary walls and they may be carried a very long way from the parent plant. In 1944 a single plant was seen in a wall at Gulval near Penzance (Cornwall) and others in gardens a considerable way from any wild stand (Hewell Grange, Worcs; Rauceby Park, Lincs); these were conceivably man-dispersed with soil. According to Salisbury (*Rep. Capac.* p. 190) the seeds are mainly dispersed in bird droppings and the contents of each berry are often deposited together, usually near some bush that serves as a convenient perch; dispersal is thus far more localized than might be expected and 'wood margins, old chalk-pits, etc., where there are bushes, are far more frequently colonized than open chalkland where bushes are usually sparse'. Average weight of seed 0.00141 g. (Salisb. *Rep. Capac.* p. 14). The seeds float in water for  $1\frac{1}{2}$  days (Praeger, quoted in Ridley, *Disp. plts.* p. 219).

(i), (j) *Viability and conditions for germination*. A proportion of the seed germinates quite well after 5 years. There is a very marked period of dormancy between September and March. If sown in September a few seeds will germinate immediately, but the remainder do not do so till the following spring. Freezing increases germination in March (Melville & Metcalfe, 1941), though in April the percentage germination is often high without freezing; for example at Oxford the average percentage germination of nine strains on moist sand in a cool greenhouse was 77% (one below 25% and five below 85%) (W. O. James). Salisbury (*Rep. Capac.*) says average germination is about 60%. Germination slow, up to 6 weeks needed under normal outdoor conditions, 14-20 days under glass at 60° F. (16° C.)

(k) *Morphology of seedlings*. The white radicle first protrudes from the apex of the seed. The epicotyl curves through 360° and then elongates, pushing its hooked self above



the soil. When about 5 mm. long (about 10 days after its first appearance), the shoot starts to unbend. The cotyledons are at first linear, but become lanceolate and finally, when they open, ovate. They are green from the time they appear above ground. The seed coat is sometimes raised on the tip of the cotyledons, sometimes retained below ground entangled by root hairs.

(l) *Effective reproduction.* Mainly by seed, but stolon production is not infrequent and new shoots may be produced from fragments of the tap root.

IX. *Parasites, diseases.* (a) *Insects and other animals feeding on the plant.* In spite of the presence of alkaloids toxic to man quite a variety of animals have been observed to feed on the leaves of *Atropa*; slugs (*Arion ater* Linn. and *Limax* spp.) and the garden snail (*Helix aspersa* Müll.) have often been collected on the plant, while among mammals, rabbits and hares devour it and sheep seem to eat it without ill effects (Furness Abbey, north Lancs), though usually they take only the yellowing leaves. *Atropa* is said to be bad for cattle.

The following insects are more or less closely associated with the plant in Great Britain (O. W. Richards):

#### COLEOPTERA

CHRYSMELIDAE: *Epitrix atropae* Foudr., larvae on roots, adult feeds on leaves and will also attack *Hyoscyamus*, local in south England (Newton, 1929). *Psylliodes hyoscyami* (L.), larva mines leaves of *Hyoscyamus*, adult will feed also on *Atropa*, locally ab. (Newton, 1934); *Psylliodes affinis* (Payle), the Potato beetle, will sometimes attack *Atropa*, at least on the Continent.

#### DIPTERA

MUSCIDAE: *Pegomyia hyoscyami* (Panz.). Larva mines the leaves; several strains of the species occur, principally on Solanaceae and Chenopodiaceae, but the *Atropa* strain is only transferable to other hosts with some difficulty (Cameron, 1914, 1916).

#### LEPIDOPTERA

The caterpillars of *Pieris brassicae* and *Mamestia* have occasionally been found on the plant.

(b) *Fungi* sp. (A. Smith). The older British literature seems practically devoid of references to fungi on *Atropa* and those recorded are mostly neither common on this host nor confined to it. Probably no fungus is of the slightest ecological importance on this plant.

#### PHYCOMYCETES

PERONOSPORALES: *Phytophthora erythroseptica* Pethyb. var. *Atropae* Alcock (Alcock, 1926) causes a root and crown disease in Scotland and has also been found in Holland.

#### FUNGI IMPERFECTI

COELOMYCETES: *Coniothyrium olivaceum* Bon. var. *Atropae* Grove is a saprophyte.

#### ASCOMYCETES

PYRENOMYCETES: *Diaporthe Chailleti* Nits has been recorded.

A virus disease on cultivated plants has been described (K. M. Smith, 1943); this causes a severe necrosis of leaves and stem under outdoor conditions. The same author later showed that *Atropa* is a symptomless carrier of *Hyoscyamus* virus 1.

In America a large number of fungi have been recorded on *Atropa* but the great majority have not been specifically identified.

*Peronospora hyoscyami* de Bary, *Phytophthora parasitica* Dastur and *Cercospora atropae* Fenne have been recorded as parasites, but only the last is specific to this host (*Plant Dis. Rep.* 1941).

X. *History*. There are no geological records. In view of the value of the plant as a drug, the limits of its natural distribution range may be the result of a combination of natural and human factors. Seeds were found among the Roman remains at Silchester (Berks) (Townsend, 1904, p. xix). The first records in British botanical literature (Clarke, 1900) are: . . . . 'In Anglia obvio preventu fruticat' (Lobel, *Adv.* p. 103) and 'It groweth very plentifully in Hollande in Lincolnshire and in the Ile of Elie at a place called Walsoken neere unto Wisbitch'. 'I found it growing without the gate of Highgate' (*Gerarde, Herbal*, 1597, p. 269).

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# BRITISH ECOLOGICAL SOCIETY

## REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1946

### Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and less Payments in advance:						
Members taking <i>Journal of Ecology</i> only ...	324	11	7			
Members taking <i>Journal of Animal Ecology</i> only ...	209	5	6			
Members taking both Journals ...	187	18	4			
Associates ...	2	5	0			
	724	0	5			
Less Reserve allocated to 1946 vol. of <i>Journal of Ecology</i> , not yet published ...	304	0	0			
	420	0	5			
Add Reserve Bt. Fd. from 1945 for 2nd parts of both Journals ...	230	0	0			
	72	0	0			
Interest on Investments ...	2	4	8			
Interest on P.O. Savings Bank Account ...	10	8	4			
	84	13	0			
<i>Journal of Ecology</i> , Sales less Cost ...	283	10	5			
Index to <i>Journal of Ecology</i> , vols. 1-20, Sales less Cost ...	2	11	9			
	£1,020	15	7			

### Journal of Ecology:

Sales: Balance of volume 33 (1945) ...	396	15	3
Back volumes and parts ...	398	5	4
Reprints of Papers ...	8	3	7
Overcharge of Insurance from 1945 ...	1	9	5

### Journal of Animal Ecology:

Sales: Balance of volume 14 (1945) ...	145	5	4
Current volume 15, 2 parts (1946) ...	327	7	0
Back volumes and parts ...	276	9	10
Reprints of papers ...	53	15	0
Grant from H. R. Napp Ltd. ...	100	0	0
	902	17	2
Balance (see above, under Expenditure) ...	336	17	7

£1,239 14 9

### Expenditure

	£	s.	d.	£	s.	d.
<i>Working Expenses:</i>						
Meeting expenses ...	31	6	1			
Printing and Stationery ...	12	13	11			
Travelling ...	12	11	6			
Clerical assistance ...	10	0	0			
Postages ...	9	6	8			
Audit Fee ...	6	6	0			
Bank Charges ...	1	0				
	82	5	2			
Grant to Freshwater Biological Association ...	10	0	0			
Subscription to Parliamentary & Scientific Committee <i>Journal of Animal Ecology</i> . Cost less Sales ...	10	10	0			
<i>Biological Flora of the British Isles:</i>	336	17	7			
Cost of Printing, Commission, etc. ...	156	2	2			
Less Sales of Reprints ...	35	17	3			
	120	4	11			
	559	17	8			
Balance—Surplus for the Year (To Balance Sheet)...	480	17	11			

£1,020 15 7

### Journal of Ecology:

Cost: Volume 33, Part 2			
Paper, Blocks, Printing and Binding ...	401	8	0
Publishers' Commission ...	97	11	4
Carriage, etc. ...	14	14	10
Editorial Expenses ...	5	14	0
Insurance of Stock ...	1	15	0

Balance (see above, under Income) ...

£804 13 7

### Journal of Animal Ecology:

Cost: Volume 14, Part 2			
Paper, Blocks, Printing and Binding ...	390	19	7
Carriage, etc. ...	7	2	4
	398	1	11
Cost: Volume 15			
Papers, Blocks, Printing and Binding ...	688	10	6
Carriage, etc. ...	21	14	1
Fee for checking references ...	10	0	0
Publishers' Commission ...	720	4	7
Insurance of Stock ...	111	1	0
	10	7	3

£1,239 14 9

# BALANCE SHEET AT 31 DECEMBER 1946

## Assets

	£	s.	d.	£	s.	d.
Cash in hand at Westminster Bank						
Current Account ... ..	189	3	2			
Deposit Account ... ..	550	0	0			
Post Office Savings Bank Account	739	3	2			
Publishing Accounts—Amounts due from Cambridge University Press:	510	8	4			
<i>Journal of Animal Ecology</i> ... ..	436	10	3			
<i>Journal of Ecology</i> ... ..	102	12	2			
<i>Biological Flora of the British Isles</i> ... ..	19	13	9			
Investments at Cost:						
£1,200 of 3½% War Loan Stock	1,230	4	1			
£700 of 3% Savings Bonds 1960/70	700	0	0			
£300 of 3% Savings Bonds 1965/75	300	0	0			
	2,230	4	1			
				£4,038	11	9

A further Asset, not valued, is the Unsold Stock of Journals, Index Volume and *Biological Flora* Reprints held by the Publishers for the Society.

VICTOR S. SUMMERHAYES  
ALEX. S. WATT  
*Hon. Treasurers.*

## Liabilities

	£	s.	d.	£	s.	d.
Members' Subscriptions, prepaid for 1947 ... ..						
Library Fund ... ..						7 10 0
Printing Accounts due to the Cambridge University Press:						1 5 0
<i>Journal of Animal Ecology</i> (3 Accounts) ... ..	341	10	3			
<i>Journal of Ecology</i> , Index Vols. 1-20 ... ..	3	4	0			
Subscription due to Parliamentary & Scientific Committee ... ..						344 14 3
Reserve of Subscriptions for 1946 allocated to <i>Journal of Ecology</i> for 1946, not yet published ... ..						10 10 0
General Revenue Account—Surplus in hand:						
Balance in hand 31 December 1945 ... ..	2,909	14	7			
Surplus for 1946 ... ..	460	17	11			
				3,370	12	6
				£4,038	11	9

Audited and found correct, and as shown by the Account Books of the Society.  
The Bank Balance has been verified by Bank Certificate, and also the Investments.

WM NORMAN & SONS  
*Chartered Accountants.*

120 BISHOPS-GATE, E.C. 2  
and  
231a HIGH ROAD, LOUGHTON, ESSEX.  
4 June 1947.



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## ARCH

8 JUL 1955  
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